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# ECOLOGICAL MONOGRAPHS

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# ECOLOGICAL MONOGRAPHS

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# ORIGIN AND DEVELOPMENT OF NATURAL FLORISTIC AREAS WITH SPECIAL REFERENCE TO NORTH AMERICA

## A SYMPOSIUM

HELD AT BOSTON, MASSACHUSETTS, DECEMBER 28, 1946

AND SPONSORED BY

THE PALEOBOTANICAL AND SYSTEMATIC SECTIONS OF THE  
BOTANICAL SOCIETY OF AMERICA

IN JOINT SESSION WITH

THE AMERICAN SOCIETY OF PLANT TAXONOMISTS, THE ECOLOGICAL  
SOCIETY OF AMERICA, AND THE SOCIETY FOR THE  
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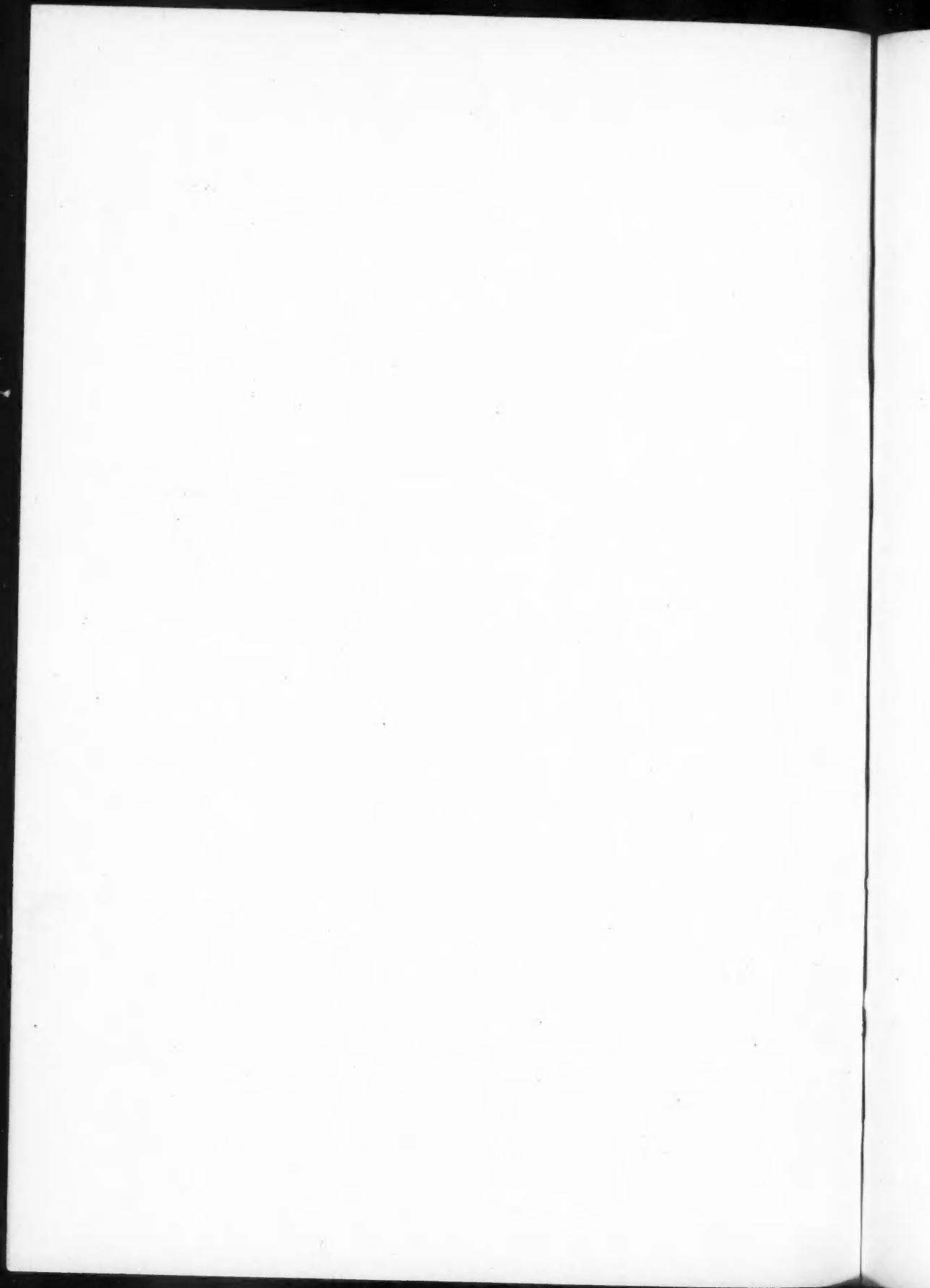
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## FOREWORD

When one travels about—be it to the other side of the world or only across a hill and into the next valley—the differences in vegetation, even between adjacent geographic and physiographic areas, become evident. Such early observations led to the recognition of natural floristic areas.<sup>1</sup> Under the influence of Humboldt, the study of plant geography took definite shape. Although there were precursors, plant ecology appears to have crystallized mainly out of the writings of Warming. For the most part both of these disciplines developed independently through the years, each building up its own concepts and sets of terminology. Although on the whole ecology was more dynamic than plant geography in its viewpoint (since it sometimes dealt with successions), many of its devotees, under the polite appellation of descriptive ecology, were studying little else than plant geography on a micro-scale. In an attempt to fix the concept of the plant association—a minor unit of the natural floristic area—in definable terms it was an easy matter for ecology to become static, almost bogged-down in classificatory terminology.

But there was a ferment in the whole field of biology which ultimately penetrated into the studies of biogeography and ecology. It began with the rapid rise in our understanding of cytology and genetics and soon spread into the study of natural populations. This yeasty ferment was a set of new concepts regarding the mechanics of speciation leading us to a wholly new vision, not only of the genetic structure of a species itself, but also of its evolution—its developmental history and potentialities for further change. These new concepts regarding species and populations, filtering over into the study of ecology and biogeography, raised a series of questions regarding the fixity of natural associations, both in space and time, and so led to a more fluid point of view on the part of various investigators.

A plant association in space is one thing; a plant association in time is quite another matter. Therefore, in an attempt to understand it in space, plant ecologists recently have begun a really serious study of plant associations against the background of time. But this involves an investigation of ancestral types and these, where known or determinable, usually are geographic disjuncts or fossil forms. This, then, brings phylogeny, paleogeography, paleoclimatology, and paleobotany directly into the sphere of ecological researches on the structure of modern plant associations. The converse is equally true, for an ecological viewpoint is necessary before conclusions concerning phylogeny, paleogeography, paleoclimatology, and paleobotany can be considered sound.

Once one of the most artificial of the classificatory sciences, paleobotany has recently come under the influence of the concepts of genetics and ecology, for since the organisms with which a paleontologist deals once were alive they certainly must have followed the same fundamental biological laws which their lineal descendants do today. But further ramifying problems arise for where, now, there is desert there once may have been a luxuriant and well-watered forest, or where arctic conditions now prevail there may once have been a lush, temperate or even subtropical vegetation. These anomalies necessitate

a further understanding of paleoclimatology, and this brings ecologists directly into the fields of geomorphology and historical geology.

Thus, today, no ecological or biogeographical study (and these fields are now so closely knit that they might well be considered parts of the same discipline) can be said to be well rounded or standing on firm ground unless it takes into account the history of the region under study in the light of its geo-structure and climate, as well as its natural biota, and the development of all these through both space and time.

In arranging this symposium effort was made to bring together discussions by those currently engaged in the study of various phases of this now wide-ranging field of modern inquiry into the backgrounds of the development of natural vegetation areas. As would be expected, the viewpoints, methods of approach, and conclusions sometimes differ considerably; this is as it should be in any healthy controversy in a rapidly developing field of research. However, in spite of any differences of interpretation, there is an obviously common objective running as a thread through this whole series of papers—the constant searching for a more complete knowledge of the influential historical events and causative biological factors underlying the dynamic phenomena operative in the ever-changing vegetational mantle of this world on which we live. This common objective is the really important thing.—W. H. CAMP.

# GEOLOGY AND PLANT DISTRIBUTION<sup>1</sup>

THEODOR JUST

*Chicago Natural History Museum  
Chicago, Illinois*

IN A SYMPOSIUM ON  
ORIGIN AND DEVELOPMENT OF NATURAL FLORISTIC AREAS  
WITH SPECIAL REFERENCE TO NORTH AMERICA

<sup>1</sup> The author is greatly indebted to Miss Nell C. Horner, Librarian, Missouri Botanical Garden, St. Louis, Mo. for arranging loans of books difficult to obtain.

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# GEOLOGY AND PLANT DISTRIBUTION

## INTRODUCTION

It has long been recognized that geological factors are much more important causes of plant distribution than are others. Thus no additional proof of this conclusion reached by De Candolle is needed here. However, the tremendous increase in our geological and botanical knowledge since the days of the early plant geographers has widened our horizon and enlarged our retrospect. With it came also many new problems awaiting their solution often before the existing ones could be solved. Thus the pertinent literature is extensive, covering as it does many borderline fields, controversial and frequently contradictory. This situation is not the outgrowth of lack of mutual understanding on the part of geologists, paleobotanists, taxonomists and others but largely the result of incomplete records and of the difficulties encountered in collecting, identifying and interpreting the necessary data. Although the whole story has not yet been worked out, this goal appears to be closer at hand than it was only some time ago.

## PALEOGEOGRAPHY AND PALEOCLIMATOLOGY

If the distribution and extent of land masses and oceans throughout geological history were known in greater detail, problems of plant distribution would offer fewer difficulties. Actually this is still one of the crucial problems confronting geology, paleontology and biogeography. Various theories have been proposed and discussed with considerable vigor but none has so far resolved all difficulties. Disregarding certain variants, the main geological theories bearing on problems of plant distribution can be grouped in the following order.

### LAND BRIDGES

Former land connections of varying extent and duration between continents have been postulated. These or some former continental masses have subsided leaving the present distribution of continents and oceans. Examples are the Austro-melanesian continent of F. Sarasin, Ihering's Archhelenis, Atlantis, etc. (Högbom 1941, Joleaud 1939, Schröter 1932, Schuchert 1932).

Although the number and extent of land bridges proposed to date can not be recounted here, it is generally conceded that former land connections did exist both in the northern and southern hemispheres (Bucher 1933, Copeland 1940, Dacqué 1932, Florin 1940, Lindsey 1940, Netolitzky 1933, Reinig 1937, Setchell 1935, Seward 1933, Skottsberg 1940, du Toit 1940). The needs of animal and plant geographers however vary sufficiently with their respective interests and so do the land bridges assumed by them. Land as such may not always be the deciding factor

in the migration of floras, for Holttum (1940) has demonstrated the effectiveness of a rather uniform climate as a barrier.

### PERMANENCE OF CONTINENTS AND OCEANS

This theory is widely accepted among geologists. Its most notable biological adherents are Darwin and Wallace. The fundamental assumption of it is that the continental land masses and oceanic basins have remained in their present position throughout geological history, though obviously with different outlines and physiographic structure. (Bucher 1933, Holmes 1944).

### CONTINENTAL DRIFT

The most disputed theories of the origin of continents and oceans are now collectively referred to as continental drift, as their common feature is the assumption of a horizontal drift of entire continental masses, regardless of the particular configuration attributed to each continent at any particular geological period (Daly 1942, Gutenberg 1939, Haddock 1936, Holland 1937, Holmes 1944, Joly 1930, Lee 1939, Longwell 1944a & b, Rastall 1929 & 1946, Schiller 1942, Tiercy 1945, du Toit 1937, Waterchoot van der Graacht 1928). According to Wulff (1943) the "permanence of the relative area of land and sea taken as a whole" is a fundamental feature of the well known theory of Wegener and may be carried over to other forms given it by various authors. For some 30 years the discussion has gone on concerning the possibility of such large scale phenomena and seems to have centered largely around the forces necessary to explain such vast changes in the earth's crust. In the opinion of Zeuner (1946) the idea of continental drift is "increasingly acceptable to geologists" who are beginning to recognize the need for horizontal movements of some sort though their intensity and rate are still subject to real scrutiny, as they would have to be about 10 to 100 times larger than the vertical ones so far readily accepted in geology.

Rastall (1946) makes the following comment: "This present writer believes that the rejection of continental drift in some form involves difficulties quite as great as its acceptance. The usual argument against it, of course, is that adequate forces are unknown. But everybody believes in the folding of mountain chains: the Alps show that it did happen, and that quite recently. But as yet we have no clear conception of what the forces were that did it. The eases surely are comparable, and it is illogical to swallow one whole and to make such a fuss about the other."

The theory of continental drift has been regarded as a fairy tale (Willis 1944), or vigorously supported with data recruited from all fields related to this complex problem. It is clear by now that the whole ques-

tion is exceedingly involved and that it can not be resolved in relatively simple and appealing terms. Thus in the opinion of some geologists (Daly 1942, Staub 1944) no major orogenies can take place without continental drift. Or, in Daly's words, "it appears that the mountain chains of the lands are by-products of the horizontal displacement of whole continents over the earth's body, and that this horizontal motion of the crust is possible only because the sub-crustal layer is nearly or quite as weak as water. Furthermore, . . . , the weak substratum is world-circling, beneath ocean as well as continent. Perhaps, too, this conclusion may yet give a basis for solving a supreme puzzle, namely, the concentration of the sial, the earth's lighter rock, in the continental sectors, leaving the oceanic sectors without any continuous cover of sialic rock." Similarly Staub (1944) rejects Wegener's particular version of continental drift but believes that the idea of moving continents is correct. According to this author, displacement of solid continental blocks is the fundamental geological phenomenon as it involves movements of the entire lithosphere. Orogenies are only partial results of this whole process though they may extend through entire geological periods after passing through prolonged preliminary phases, viz., the Alps and other mountain ranges. This conclusion is essentially the same as that reached by Longwell (1944) who says: "in the genetic study of major earth-features I can not believe we have arrived at a stage that permits discarding the method of multiple hypothesis."

Staub's summary (1944) provides a good example of such an hypothesis. It reads as follows: "Neither contraction alone, as classical geology assumed, nor equatorial drift or a primarily western drift, as Wegener thought, nor magmatic movements alone, as suggested by Otto Ampferer 40 years ago in opposition to the theory of contraction, evoke the complicated mechanism of crustal movements and of tectogenesis on earth. Rather all of these factors are integrated, complement each other, follow or release each other throughout geological history. As a result, contraction of the earth is still going on. Equatorial drift away from the poles directs the migrating masses as on other celestial bodies; magmatic movements contribute to these movements tending toward isostasy; the decomposition of radioactive substances, in addition to isostatic processes and further contraction of the planet, continually revives the otherwise slackening movements. Therefore we know now:

"Neither the theory of contraction as such nor continental movements caused solely by equatorial drift nor magmatic movements can independently account for crustal movements; rather all of these factors are integrated into a grand interplay of forces producing the tectonic phenomena of the earth. . . ."

#### SHIFTS OF CLIMATIC BELTS

Intimately associated with problems of paleogeography are those relating to the climates of the past (Brockmann-Jerosch 1914, Brooks 1926, Dacqué 1932, Eckardt 1925, Kerner 1930, Kubart 1929, Seward

1933). Fossils have been found far out of range of occurrence of their nearest living relatives (Berry 1920, 1930, 1945, Gothan 1924, *et al.*). There is also other evidence which speaks for different climates in various geological periods and their different distribution on the globe. Some periods, particularly the Jurassic, seem to be characterized by greater uniformity of climate (Gothan 1924), whereas the paleobotanical evidence indicates a certain zonation for others. The first sign of such is found in the Permo-Carboniferous floras of Asia studied by Halle (1937).

A shifting of the climatic belts is commonly assumed, particularly in conjunction with continental drift and its accompanying movements of the poles and the earth's axis. For example, Simpson *et al.* (1930) concluded that the "most cogent argument that has been offered in favor of continental drift" is the fact that "widespread ice caps reached to low latitudes in the southern continents." Halle (1937) on the other hand has difficulty in the interpretation of the eastern Asiatic Permo-Carboniferous floras in the light of continental drift. Similarly, other paleobotanists encounter difficulties with continental drift as a basis for the explanation of the distribution of fossil plants (Høeg 1937, Gothan, *et al.*). It should be pointed out however that many paleobotanists are favorable to continental drift (Hirmer 1938, 1942, Mägdefrau 1942, Sahni 1936, Zimmermann 1930, *et al.*) or at least expectant of future verification by geophysical research (Seward 1933, 1939).

Umbgrove (1946) has recently reviewed various theories on polar displacement and shown that calculations by Milankovitch used in support of Köppen-Wegener's findings are in error. Other interpretations and details given by him are inconclusive and of no immediate bearing in this connection. Berry (1945) adds a note of caution and even challenges meteorologists "gifted with sufficient knowledge" to discuss the effects in the late Paleozoic of a wide Mediterranean Sea (Tethys) and an enormous southern continent. Finally, Zeuner (1946) made some rough estimates of the supposed movement of the equator relative to shifting climatic zones. He found that since the Tertiary the equator would have had to move at a rate of 4500 km. in 50 million years, or 9 cm. per year, from Spain southward in order to reach its present position. Seward (1933) has raised the question of the reliability of plants as "thermometers of the ages." The great care needed in the study of fossil plants has been repeatedly demonstrated and examples are given elsewhere in this paper. In short, our knowledge of the climates of the past is far from being complete and greatly in need of additional records and interpretation.

#### RHYTHMS OF GEOLOGICAL PHENOMENA

Although the forces responsible for many geological phenomena are still unknown or poorly understood, there is considerable evidence of their periodic operation and rhythmic occurrence (Grabau 1940, Seward 1933, Umbgrove 1942). This is at least one of the fundamental assumptions of Haarmann's oscil-

lation theory of diastrophism (see Longwell 1930). Umbgrove (1942) gives a more detailed account of the many ways in which this periodicity in earth history is demonstrated. He distinguishes four major periods, each extending about 250 million years, and some 25 minor periods of diastrophism and concludes that "diastrophism is going on all the time somewhere in the world, which seems reasonable if we consider that the ultimate causes, whatever they may be, are probably always in operation." The possibility of continental drift as seen by Wegener and du Toit is rejected by Umbgrove in view of the thin sial layer found on the floor of the Atlantic and Indian oceans which would prevent sialic continents from moving through it. But Rastall promptly points out that "icebergs can plough through pack-ice." Ice ages also seem to follow this major periodicity of 250 million years, the period between the Karroo Ice Age of the late Carboniferous and Pleistocene, and are roughly contemporaneous with major orogenies. Umbgrove claims that these cycles are linked with cosmic causes, including the rotation of the galaxy. While these explanations may well be far removed from the immediate considerations of the plant geographer, it is equally true that repeatedly recourse has been made to such causes as possible evolutionary factors as will be shown below.

Thus a certain periodicity of geological phenomena seems well established. But it is not at all clear what bearing it had on the evolution of organic life beyond the repeated speculation of the effect of the main orogenies on accelerating the rate of evolutionary processes and the slowing down of the latter during more quiet geological periods (Rubtsov 1945).

#### GEOLOGICAL PROCESSES AS EVOLUTIONARY FACTORS

The notion that geological processes are effective evolutionary factors has appeared often, ranging from the outmoded cataclysmic theory of Cuvier to various recent versions. Schindewolf (1937) in his review of the more important contributions to this problem concludes that neither macro- nor mega-evolution could be attributed directly to the action of geological phenomena though local physiographic changes may readily be involved in micro-evolution or speciation. Thus new habitats are frequently provided by tectonic phenomena, though they can hardly be said to induce evolution on a major scale. While some indirect effects of tectonic phenomena like changes in climatic zonation, opening and closing of migration routes, etc., may be far-reaching, they are not the real causes of the disappearance of major groups of wide distribution. It seems that other, possibly internal, causes are here involved.

Similarly, volcanic phenomena are limited in occurrence and often even more local in character. The classic case of the eruption of the Krakatau has shown this clearly, for the island was invaded by the old flora and fauna and not by new types. Thus the old Buffonian concept postulating direct effects of

geological processes on the evolution of plants and animals is untenable though the remote possibility of local micro-evolutionary effects remains.

In Schindewolf's opinion, cosmic causes with world-wide effects on every ecological niche would be required to induce evolution in many groups at the same time and without their pursuing any special evolutionary course. Changes in the intensity and nature of light and heat rays have been suggested in this connection, for they are believed to bring about periods of increased mutability and effect profound changes of germ plasm. Events of this sort seem to have taken place at the beginning of the Permian and the close of the Cretaceous.

Rubtsov (1945) on the other hand attributes acceleration of evolutionary processes as indicated at the boundaries of various geological periods to the profound effects of orogenetic processes, whereas quiet periods are generally marked by slow evolution. Similarly, areas subjected to great geographical changes are said to show the result of more rapid evolution, viz., both sides of the Atlantic are supposedly characterized by a greater abundance of phylogenetically higher groups while eastern Asia is now a refuge of many old and elsewhere extinct forms. By comparison, Berry (1945) questions the possibility of the sudden change in the fossil floras from Paleozoic to Mesozoic and offers as an alternative interpretation that this change was "a gradual transition foreshortened by our imperfect knowledge into seeming suddenness."

#### ORIGIN AND TYPES OF AREAS

Plant distribution is usually recorded by the various forms of areas occupied by plants such as relie, vicarious, discontinuous, progressive (expanding) and contracting (retrogressive) areas (see Wulff 1943, Cain 1944, Hayek 1926). In this context the relie and discontinuous areas are of greatest interest as their interpretation involves major geological events and theories as well as paleoclimatological considerations. Various botanists (Campbell 1943, 1944, Hirmer 1938, 1942, Irmischer 1922, 1929, Koch 1924-1933, Studt 1926, Herzog 1926, Mägdefrau 1942 and others) have accumulated voluminous data from living and fossil plant distribution in support of continental drift. The last to join these ranks is Hutchinson (1946) who states his case clearly: "As a botanist who has studied the distribution of plants for many years, particularly African plants, I am a firm believer in Wegener's ideas." However, not all botanists are convinced of the validity of continental drift as the sole explanation of discontinuous areas and have voiced strong objections (Diels 1928, 1934, Fernald 1944, Merrill 1943, Schuster 1931, Suessenguth 1938, Berry and others). As is to be expected, often the same group of plants is used to illustrate both sides of the controversy, viz., the Cycadaceae (Koch 1925 vs. Schuster 1931).

The greatest difficulty in interpretation is offered by the largest discontinuous areas known, e.g., the so-called austral or subantarctic disjuncts. Schröter

(1932) gives five possible explanations proposed at different times and from different points of view. The whole question is linked, if not identical, with the problem of the bipolar distribution and origin of modern floras (Campbell 1943, 1944, Du Rietz 1940, Florin 1940). Hutchinson (1946) for instance regards the families of flowering plants and smaller groups peculiar to South Africa and some to Australia as well as "*austral types evolved independently in the Southern Hemisphere.*" Similarly, Florin (1940) favors "from the Permian onwards" two major centers of development of modern conifers, one of which is definitely southern and has left no trace of representatives in the northern hemisphere.

The critical point in most of these discussions is the possibility and probability of the following four processes, monotypy, monophyly, polytypy and polyphyly. As it is impossible to review here the entire controversy (see also Cain 1944 and Schröter 1932), the following remarks must be limited to the strong suggestion made by Suessenguth (1938) regarding the origin of the large areas occupied by entire plant families. This author is of the opinion that certain areas can be explained best by assuming the possibility of a polytypic as well as polyphyletic origin, provided the original stock was sufficiently widely distributed. According to this view, several or even many parallel lines are evolving more or less simultaneously in several species or genera. This mode of origin would do away with the problem of large scale migrations and the invariably long spans of time required for such. Unfortunately, not a single case is presented by Suessenguth to illustrate this view. Rather he offers immediately as a possible objection to this mode of origin the discontinuous areas occupied by such groups as the Cycadaceae, Gnetaceae, Balanophoraceae, etc. all of which are treated as contracting areas. Conversely, plant families characterized by expanding areas are said to have reached their maximum extent if the family is supposedly phylogenetically younger, viz., Gramineae, Cyperaceae, Umbelliferae, Labiatae, Compositae etc. Here, apparently, fossil records would aid greatly in determining the relative phylogenetic age of the major angiosperm groups, as it can not be stated categorically that the Compositae for instance may not be as old as many other old angiosperm stocks.

#### MODERN FLORAS AND THEIR ANALYSES

Detailed analyses of known fossil (Goodspeed *et al.* 1936, Gothan 1937, Hirmer 1935-1942, Seward 1933) and living floras have yielded striking, though not always conclusive results. Customarily floras are divided into elements, either geographical, genetical or otherwise, depending on the particular needs or reasons for study. Excellent examples are the careful studies of the British flora by Matthews (1946), the South African flora by Weimarek (1941), the flora of Asia Minor by Schwarz (1937), the flora of the Pacific islands and adjacent Asia by Andrews (1940). Hu (1940), Kanchira (1940), Lam (1938, 1940),

Merrill (1926), Ridley (1937), Setchell (1935), Skottsberg (1940) and Tardien-Blot (1940).

As it is impossible to treat all methods employed in the analysis of floras, only representative examples are given here.

#### STATISTICAL METHODS

In his detailed analysis of the Post-Pleistocene flora of the eastern Baltic area Kupffer (1930) used various statistical criteria. He characterized the flora of this area in terms of its floristic dissimilarity (ratio of species limited to this area *versus* all species occurring there), its similarity (number of species in common with one or more areas of comparison), and its floristic gradient (expressed in terms of distance within or outside the area studied). Other statistical methods are reviewed by Cain (1944).

Following his intensive studies of the distribution of the insect order Homoptera Metcalf (1946) found "a correlation between zoogeographic regions and taxonomic groups." Apparently no group of plants has ever been analyzed from this point of view.

The elaborate task of dividing the world into regions on the basis of the number of species of flowering plants represented in each was attempted by Wulff (1937). Fully cognizant of the multitude of possible errors in delimiting species etc., Wulff established five classes differing in the number of species represented in areas referred to these. They are: 1) none to 500 species, 2) 500 to 2,000 species, 3) 2,000 to 3,000 species, 4) 3,000 to 7,000 or 8,000 species, and 5) more than 8,000 species. From the map prepared on the basis of his analyses Wulff was able to draw some general conclusions. Generally the number of species increases from the polar regions toward the equator with the general increase in temperature in that direction, although subtropical steppe and desert areas have fairly low numbers of species in view of their great aridity. In Europe and North Africa the number of species decreases for the same reason from W to E, whereas in temperate Asia the reverse is true, namely, from E to W. Mountainous areas are generally characterized by larger numbers of species in view of the greater humidity, physiographic changes in relief and soil, limited competition and the presence of Tertiary relics. The greatest climatic changes since the Tertiary have taken place in the polar and temperate areas accompanied by a complete change of the plant world represented in the fossil record and found there now. By comparison, the tropics and subtropics retained almost unchanged ecological conditions, accompanied by a virtually uninterrupted evolution of their floras. This is especially true of southeastern Asia and South America whose floras may range from 20,000 to 45,000 species and are thus the richest known floras of the world. Tropical Africa apparently witnessed fewer changes and its flora is therefore poorer in species ranging from 10,000 to 15,000 species. The Mediterranean area, southeastern and southwestern North America were characterized by more favorable climatic conditions and therefore retained a large part of the Tertiary flora.



## ECOLOGICAL METHODS

These have been widely employed by paleobotanists and others though inherent dangers of misinterpretation are always present (Berry 1945, Cain 1944, Chaney in Goodspeed 1936, Brockmann-Jerosch 1914, Gothan 1924, Seward 1933, Weiss 1925). In an effort to avoid erroneous interpretations made on the basis of limited comparisons, Bews (1927) analyzed all known fossil angiosperms ecologically and statistically. He compared entire groups of fossils with modern types of vegetation regarding leaf size, margin, texture, etc. Hansen (1930) has shown that the groups and genera of greatest fossil age are now represented only by phanerophytes, whereas genera of Miocene or Pleistocene age are today represented by an increasing percentage of chamaephytes, hemi-cryptophytes, and therophytes. Any disharmony between climatic periodicity and phasic development in plants in a given area is regarded by Scharfetter (1922) and Fritzsche (1936) as proof of the origin of these plants in other areas. Wulff (1943) is of the opinion that the evidence in this connection is inconclusive as it omits the possibility of change *in situ*.

## HISTORICAL (GENETICAL) METHODS

Long ago Blytt (1882) stated that "present day vegetation reflects, as in a mirror, the geological history of a country, different groupings of species being the expression of different stages in that history." Since then the science of areography (Cain 1944) or phytogeography (Reinig 1937, 1938, Schwarz 1937) has been developed and its aims and methods variously defined. For example, Reinig (1939) recognizes two major principles of chorology, namely, constant dependence on habitat, and monotonous origin of systematic forms. Working on an entire flora, viz., that of Asia Minor, Schwarz (1937) used various new and old concepts and demonstrated their applicability as far as possible. These concepts are: primary, secondary, relic and migrant floras, relic areas (refuges), centers of origin, and two major phases of evolution, viz., progressive and retrograde. Relic floras are relatively young with reference to their ecological environment, though largely composed of fairly old stocks; the species may be of rather recent origin, since speciation goes on continuously; the areas however are old. Migrant floras on the other hand are the youngest floras and are composed of species of divergent relationships and distribution. Usually the appearance of a migrant flora disturbs the sociological equilibrium bringing about definite deterioration of ecological conditions. In this case migrant floras may be regarded as retrograde. Only after the sociological equilibrium has been re-established, can the migrant flora begin to function as a new (secondary) center of origin. Centers of origin are either primary or secondary. Primary centers are characterized by an abundance of related though well marked species and of forms intermediate between those isolated in the relic areas. Here the ecological conditions are relatively stable and speciation

is thus solely the expression of the available genetic material and of continued mutations and recombination as well as dispersal. Primary floras are made up of very old stock though composed of relatively young species, the product of almost uninterrupted speciation. The areas in turn are very old. Gene filters appear where relic or primary floras come in contact. Here geographical clines appear, which are followed by the breakdown of the species and recombination of their entities, and often by new evolutionary outbursts. Gradually gene filters either absorb entirely the old floras or become wholly or partly isolated and thus begin to function as secondary centers of origin. These in turn are populated by secondary floras composed of species of heterogeneous origin and relationship. Migrant floras indicate that contact has been established between relic areas, poor in biotypes, and centers of origin which are comparatively rich in biotypes, and that migration has started in the direction of least resistance, e.g., toward relic areas. Thus migrant floras are the youngest floras, as indicated above. Each of these phases may be regarded as a stage in the development of a modern flora, very much like geological strata mark subsequent periods of earth history. Thus any area may eventually be characterized by its "chorogenetic spectrum" rather than as a mere geographic entity. At present no one flora represents all of these possible stages but is likely to be the result of several.

## CENTERS OF ORIGIN AND DISPERSAL

As Cain (1944) has formulated the important criteria for indication of center of origin, this discussion can be restricted to the general problems connected with the origin of vascular floras. As far as our modern floras are concerned, two main theories are to be considered.

Generally Heer (1868) is given credit for proposing the theory of the polar origin of our modern floras, particularly its most widely accepted form, viz., that of the monopolar (boreal) origin of floras in the northern hemisphere. It is also known as the monoboreal relic hypothesis (of Thiselton-Dyer, Lydekker et al., see Schröter 1932). According to it, the northern hemisphere is the center of origin of all floras and faunas whence they migrated southward in successive waves and left their relic members in the southern hemisphere. The broad latitudinal distribution of boreal organisms (holartetic) is said to account for their migration southward into the three southern continents and their analogous development there. Considerable paleobotanical evidence has been accumulated that apparently serves to strengthen this widely held theory (Engel 1943, Harris 1937, Hirmer 1942, Koch 1924-1933a, Seward 1939, Stebbins 1940). The alternate possibility of a bipolar origin, previously referred to, is gaining ground, at least for certain groups and periods (Du Rietz 1940, Florin 1940). The extreme view of the bipolar origin of temperate floras held by Campbell (1943, 1944) is based on du Toit's assumption of two primordial

continents, Laurasia and Gondwana. Hutchinson (1946) also assumes an austral origin of the families and groups confined to the southern hemisphere.

The earliest history of known vascular (pteridophyte) floras is too poorly known to permit any specific statement regarding their origin, as the entire period from the appearance of the pteridophytes in the Upper Silurian to the end of the Lower Carboniferous is marked by the great uniformity of its plant life (Hirmer 1938). With the Upper Carboniferous, however, and prior to the beginning of the Permian, fairly distinct floral regions can be recognized, at least in eastern Asia (Halle 1937). These regions are: a) Euramerican region: comprising Europe and North America, b) Angara region: extending from the rivers Dwina and Petschora in the west to the Kusnezsk and Minnussinsk coal basins, c) Cathaysia region: comprising Shansi and Korea; the most typical plant life of this region occurred in the Upper Carboniferous and Lower Permian; an Upper Carboniferous (Stephanian) flora of Sumatra may also belong here, and d) Gondwana region: including central and southern South America, Antarctica, southern and central Africa, India south of the Himalayas, Australia with Tasmania and New Zealand. The famous Gondwana flora was essentially confined to the Gondwana region from the end of the Carboniferous throughout the Permian. The only connections during this time were apparently those with the Angara region. With the beginning of the Triassic Gondwana elements entered the Euramerican region and conversely Euramerican elements migrated southward. These contrasts of the northern Arcto-Carboniferous flora and the Glossopteris flora of the Gondwana region can not be explained by continental drift in the opinion of Halle, though Hirmer thinks so.

At the end of the Triassic and prior to the beginning of the Jurassic plant life is once more characterized by considerable uniformity. Throughout most of the Mesozoic the floras of the southern continents are quite uniform, a fact regarded by Hirmer as evidence in support of continental drift. Signs of latitudinal zonation of the subtropical flora, extending into the Arctic, make their appearance during the Upper Cretaceous and Lower Tertiary. These generalizations could be substantiated by including evidence drawn from the distribution of fossil gymnosperms.

Studies by Seward and Conway (1935a & b) of the Cretaceous strata of western Greenland have yielded some striking results. Here extensive beds bearing remarkable plant fossils are found, but are difficult to separate into the usual stratigraphic units. The most significant result seems to be the fact that many plants belonging to the preceding Jurassic and Wealden formations are accompanied by the first known flowering plants. Thus the first angiosperms appear in a vegetation otherwise composed of Mesozoic ferns and gymnosperms. The uppermost (Patoot) strata contain more Dicotyledones than do the lowest (Kome). It seems that the Cretaceous plants of western Greenland with their ancient character constitute remnants of the vegetation known from the

Rhaetic and Liassic deposits of eastern Greenland (Harris 1937, Seward & Conway 1935), although no direct connection between them is known. Conspicuous among the old Jurassic and Wealden types of almost cosmopolitan distribution are the Gleicheniaceae, Matoniaceae, Dipteridaceae, Cycadophyta *s.l.*, and Coniferae.

Seward and Conway believe that the angiosperms originated in the Arctic and that the geographic and climatological conditions of Greenland as well as the geological ones during the Cretaceous were conducive to the origin and rapid evolution of the angiosperms. Greenland was then probably part of a much larger continent covered with vegetation for the most part and, on the whole, less disturbed or threatened by the Cenomanian transgression than areas south of it. Proximity to the pole is regarded as productive of new types due to increased activity during the northern summer and a prolonged rest period during long winters with higher temperatures than are known from there today. From this center the angiosperms are believed to have spread southward in Eurasia and America.

Comparison of these floras with others of comparable age and composition is difficult indeed, for the Greenland floras are the only known mixed floras of this kind, containing Mesozoic ferns and gymnosperms as well as the earliest angiosperms. The latter are quite similar to modern types. Because of this mixed character, the Cretaceous floras of Greenland cannot be assigned to Lower and Upper Cretaceous strata as is customary elsewhere. The slight resemblance of the floras of the Potomac formations of the coastal plains of the eastern United States is attributable to their poor representation of Mesozoic types and the appearance of angiosperms in the uppermost strata, whereas the Greenland beds contain angiosperms even in the lowest strata. Likewise other American Cretaceous floras lack older pteridophyte and gymnospermous types but consist mainly of angiosperms (New Jersey, Gulf States, Dakotas). Approximately contemporaneous Eurasian floras too are not as rich as the Greenland floras.

The climate of that time was apparently more or less subtropical though many deciduous trees were represented. In Seward's opinion a small movement of the earth's crust could account for this climate even if the pole remained stationary. At the same time it must be assumed that different oceanic conditions prevailed permitting warm currents to reach the shores of Greenland. For instance, an increase of eight degrees in winter and of four degrees in summer today would provide Norway at a latitude of 65 degrees N with a subtropical climate such as is found on the northern island of New Zealand. Moreover, the climate of the area occupied at present by any plant does not always indicate fully the plant's ecological requirements. The genus *Platanus*, though definitely more southern in distribution, can withstand the coldest winter in Europe as demonstrated by transplants. *Ginkgo*, *Sciadopitys* and other genera behave likewise.

Hollick's extensive studies (*vide* Hirmer 1942) of the Upper Cretaceous and Eocene floras of Alaska disclosed that the Mesozoic types contained resemble those found in Bohemia and Sachalin and thus fit in general the concept of the Arctic origin of modern floras. These floras too are subtropical in character, and show a close relationship to the modern floras of North America, Europe and East Asia including even Australasia.

The great expansion of the angiosperms took place during the early Tertiary. This event is described in one of Seward's (1939) addresses and may fittingly be quoted here: "The fossil flora of Mull represents an early phase of what may be called the modern type of vegetation, which overspread the world in the later stages of the Cretaceous period and has persisted with few major modifications until now. Evolution seems to have been characterized by bursts of production when new and successful types exercised a transforming influence; and these periods of exceptional creative activity were separated by periods of relative stability. The early Tertiary floras belong to a stage when a new order had become well established and an older order had passed its prime. The one great difference that emerges from comparison of the Mull flora and the existing European floras is not a difference in the components of the world forests but a contrast in the geographical positions occupied by the various genera in the northern hemisphere; for the most part a western home has been exchanged for a home in the Far East."

But with all Berry (1945) seems to be right in his appraisal of our knowledge when he says: "In spite of the great volume of descriptive literature of modern paleobotany and the light which it has shed on geological problems and plant history, it has been a history of modern families and not of the founders of dynasties."

#### SUMMARY

1. Geologists are not agreed on the interpretation of the origin and development of continental masses and oceans. A modified form of the theory of continental drift may prove acceptable if shown to be connected with diastrophism.

2. Many data pertaining to fossil and living plant distribution, especially large discontinuous areas, have been interpreted in the light of continental drift. Other data can not be construed as evidence in support of it.

3. Available information concerning the earliest known angiosperm records from the Cretaceous of Greenland indicates an Arctic center of origin, the existence of a subtropical flora of wide distribution composed of many old stocks and their subsequent southward migration. These facts can be used as evidence in favor of the theory of the monoboreal (northern) origin of modern angiosperm floras.

4. A bipolar evolution of certain stocks, notably of the conifers, appears quite probable, at least of their modern representatives.

5. Evolution has apparently been characterized "by

bursts of production" that were followed "by periods of relative stability."

6. The composition of modern floras is exceedingly complex due to the interaction of many known and unknown processes such as climatic changes and migrations, as the members vary in age and origin. Only detailed analysis of all fossil and living members can disclose the true composition and history of modern floras.

7. With few exceptions the old doctrine of historical plant geography is apparently still valid: areal continuity presupposes genetic continuity.

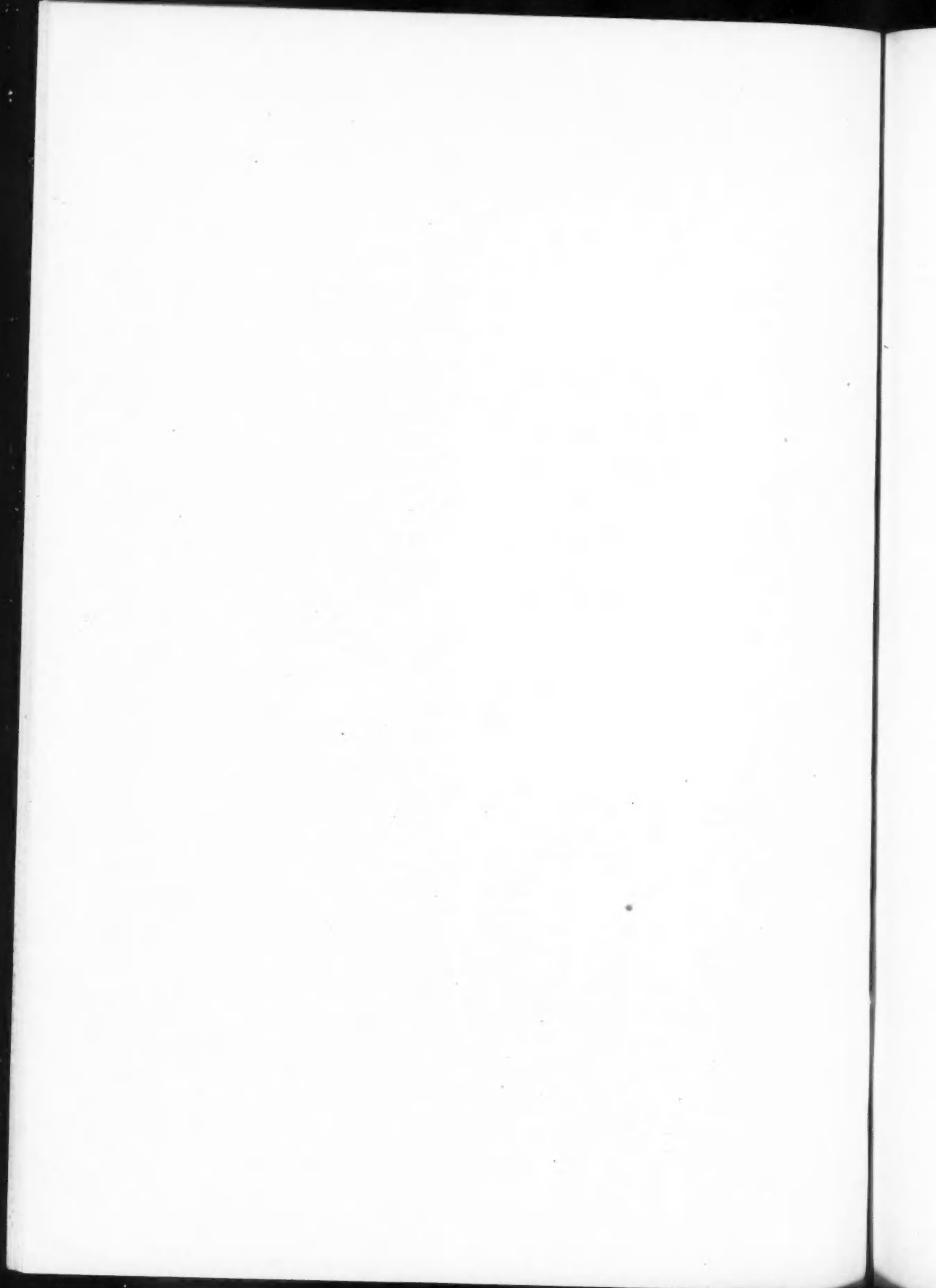
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TERTIARY CENTERS AND MIGRATION ROUTES

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IN A SYMPOSIUM ON  
ORIGIN AND DEVELOPMENT OF NATURAL FLORISTIC AREAS  
WITH SPECIAL REFERENCE TO NORTH AMERICA

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## TERTIARY CENTERS AND MIGRATION ROUTES

### INTRODUCTION

The rocks of the Tertiary system provide the most reliable data now available for initiating a discussion of early centers of distribution of land plants of modern types. The stratigraphic sequence of its continental deposits is more complete than in older rocks, and its fossils more readily assignable to modern families and genera than those of older floras. The ultimate origin of angiosperms is not clearly indicated by the Mesozoic record; much collecting by paleobotanists, followed by broad investigations both by paleobotanists and botanists, must precede our understanding of the nature and relationships of the earliest angiosperms, and our designation of the area or areas from which they have spread out to colonize the earth. By contrast, the composition and distribution of Cenozoic floras are already well known, particularly in the northern hemisphere.

In this paper I shall review the distribution of Tertiary vegetation in North America and elsewhere. Particular emphasis will be placed on the larger and longer-lived units of vegetation (Floras), as distinct from the more local and transient units (floras). It is these larger units, such as the Arcto-Tertiary Flora, which have migrated for thousands of miles, over a span of time to be measured in tens of millions of years. During such movements in space and time they have been altered in many details, but they have retained their essential elements and components to a marked degree. This conservatism makes possible our recognition of the Arcto-Tertiary composition of forests growing at middle latitudes in the northern hemisphere today; it provides a basis for projecting back for some 60 million years, northward for more than a thousand miles, the temperate climates now found in the United States; for the Arcto-Tertiary Flora of the Eocene epoch lived in Alaska and Greenland during a milder climatic regime than characterizes the high latitudes in our day. Similar projection backward may be made for the Neotropical-Tertiary Flora of middle latitudes; the modern forests of Mexico and Central America are its direct lineal descendants, and enable us to reconstruct an early Tertiary environment characterized by higher temperature and precipitation than is found today in Oregon and California.

Interpretation of the significance of shifting forest distribution during later geologic time must depend not upon a single flora from a limited area, nor upon the evidence of a few plants, no matter how suggestive their present habits may be. The factors which brought such profound changes must have been worldwide in operation, and must have affected whole plant populations. I shall therefore discuss the composition, changes in distribution, and inter-relations of

the better known major units of vegetation of the Tertiary period. These units are the Neotropical Tertiary Flora of middle and low latitudes in the Americas, the Paleotropical-Tertiary Flora from the same latitudes in the Old World, the Arcto-Tertiary Flora of high northern latitudes, the Antarcto-Tertiary Flora of high southern latitudes, and the Madro-Tertiary Flora of the Southwest.

### NEOTROPICAL-TERTIARY FLORA

#### PRELIMINARY REMARKS

Best known from older Tertiary deposits of the United States, this Flora is largely represented by leaf impressions of angiosperms. At the type locality of the Clarno flora in Oregon and in the Brandon lignite of Vermont, there are abundant fruits some of which show internal structure; a few stems have been studied, but relatively little is known regarding organs other than leaves.

The leaf characters of these Eocene and early Oligocene fossils suggest relationships to plants now living in the tropics. Leaves are of relatively large size, with thick texture suggesting an evergreen habit; a majority have entire margins, and species with elongate tips are numerous. Table 1 gives the percentages of these characters shown by the leaves of several Tertiary floras, with corresponding data from modern floras.

TABLE 1. Leaf characters of west American dicotyledons, showing percentages.

	Length		Margin		Dripping Point		Texture	
	Over 10 cm.	Under 10 cm.	Entire	Non-entire	Present	Absent	Thick	Thin
Panama, Recent Tropical (41 species).....	56	44	88	12	76	24	98	2
Comstock, Upper Eocene (25 species).....	56	44	76	24	60	40	92	8
Goshen, E-Oligocene (40 species).....	53	47	61	39	47	53	98	2
Weaverville, Lower Oligocene (36 species).....	60	40	47	53	49	51	57	43
Bridge Creek, Upper Oligocene (20 species).....	30	70	15	85	10	90	54	46
California, Recent Temperate (22 species).....	27	73	23	77	9	91	64	36

Closer resemblance of older Tertiary plants to those now living in the tropics, rather than to those of temperate America, seems readily apparent from these and other available data on characters of fossil leaves.

A second basis for establishing the nature of past floras and their environments is to determine the systematic relationships of plant fossils. Comparisons with leaves, fruits and stems of living plants have

led to assignment of most older Tertiary plants from middle latitudes to genera and families now characteristic of forests living nearer the equator. Some of these are now wholly confined to low latitudes; examples are the Burseraceae (Canarium), Combretaceae (Terminalia), Dilleniaceae (Actinidia, Davilla, Dillenia, Tetracera), Meliaceae (Carapa, Cedrela), Monimiaceae (Siparuna) and Sabiaceae (Meliosma). Perhaps the most characteristic Eocene family, the Lauraceae (Acrodiclidium, Cinnamomum, Cryptocarya, Laurus, Lindera, Machilus, Nectandra, Neolitsea, Ocotea, Persea) is represented in the United States today by only a few genera, mostly shrubs or small trees which are largely confined to southern Florida; the only typically temperate members of the family are Lindera and Sassafras of the eastern United States, and Umbellularia in the West; with the exception of the last two, no arborescent members of the Lauraceae may be said to be common or widely distributed in temperate North America at the present time.

A considerable number of vines and shrubs in living forests at temperate latitudes may be interpreted as survivors of families whose Tertiary distribution extended farther north. The Araliaceae is represented today by Aralia and Echinopanax, both shrubs; Anonaceae by Asimina, a shrub; Bignoniaceae by Bignonia, a vine; Celastraceae by Celastrus and Euonymus, shrubs; Sterculiaceae by Fremontia, a shrub. All of these families were represented by additional genera during older Tertiary time, and the fossil record indicates an arborescent habit for the majority of their members. Other families such as the Boraginaceae, Euphorbiaceae and Leguminosae, whose habit was tree-like during the Eocene, are for the most part herbaceous in middle latitudes at the present time; their Eocene members, now largely tropical in distribution, were Cordia, Ehretia (Boraginaceae); Acalypha, Alchornea, Aporosa, Drypetes, Mallotus, Sapium (Euphorbiaceae); Acacia, Caesalpinia, Cassia, Canavalia, Dalbergia, Desmodium, Inga, Lonchocarpus, Pithecolobium, Pongamia, Sophora, Strongylodon, Vouapa (Leguminosae). While many Neotropical-Tertiary floras include typically temperate genera such as Diospyros, Liquidambar, Platanus, Quercus and Viburnum, all of these commonly range into the tropics today, occurring largely on mountain slopes. The composition of these older floras of middle latitudes is strongly indicative of a climate now found some twenty degrees of latitude to the south.

To botanists who are skeptical regarding the soundness of generic determinations based solely on fossil leaves—and their skepticism may reflect inadequate knowledge of leaf characters of modern plants—we may point out that even though the above mentioned generic and family assignments are incorrect, there is an independent basis for our conclusion that older Tertiary climate was subtropical in regions of North America now temperate. For the size, margin, shape and texture of the fossil leaves indicate absence of

frost and high precipitation at middle latitudes, as above suggested.

The more important examples of the Neotropical-Tertiary Flora in North America are:

*Wilcox flora*, from the Lower Eocene of the Mississippi embayment in the southern United States (Berry 1916a, 1930, 1937, Ball 1931).—180 genera have been recognized, most of which appear to be valid; over-multiplication of species by Berry and others has brought the total to between five and six hundred, of which probably not more than half represent distinguishable and recognizable units of vegetation. "The flora is largely coastal and indicates a warm temperate climate and an abundant rainfall, more tropical in its facies than that of the late Upper Cretaceous which preceded it in this same region" (Berry 1937, p. 35). Evidence has been presented (Berry 1930, pp. 25-29, Berry 1937, p. 36) which indicates that the vegetation of the eastern side of the embayment was derived largely from the Antillean area, while that on the western side shows greater affinities with the living floras of Mexico and Central America.

*Claiborne flora*, from the Middle Eocene of the Mississippi embayment, and the *Jackson flora*, from the Upper Eocene of the same region (Berry 1924, 1937).—These floras, smaller than the Wilcox, indicate progressively warmer climate in a coastal habitat, and a similar origin to the south.

*Brandon flora*, from the Eocene of Vermont.—Berry (1919) has presented evidence that this assemblage, represented by fruits, seeds and wood, lived on the borders of an inland basin at about the same time as the Jackson, and under similar, though perhaps more temperate, physical conditions.

*Catahoula flora*, from the Oligocene of the southern states (Berry 1916d).—24 species assigned to 15 genera make up this relatively small assemblage, which Berry believes to indicate a continuation of subtropical strand conditions.

*Raton, Denver, and Fort Union floras* from the Lower Eocene (Paleocene) of the Rocky Mountain area (Knowlton 1917, 1930; Newberry 1898).—These interior floras, of approximately the same age, require restudy employing present-day methods before they can be adequately interpreted.<sup>1</sup> Preliminary survey by the writer (Clements & Chaney 1936, pp. 8-10) has indicated a marked decrease in subtropical representation from the Raton in New Mexico to the Fort Union in Montana. Presence of numerous temperate genera in the Fort Union indicate that it bears an ecotonal relationship between the Arcto-Tertiary Flora of western Canada and Alaska, and the more typical Neotropical-Tertiary Flora to the south.

*Green River flora* from the Middle Eocene of the Rocky Mountain area.—Brown's revision (1934) of this flora, together with the pollen studies of Wodehouse (Wodehouse 1933), indicates that the forest which lived near an inland basin of deposition, at an elevation of 3,000 feet or less, was of a warm-temperate type with local evidences of aridity. Several

<sup>1</sup> Study of these floras by R. W. Brown is nearing completion.



floras of possible Upper Eocene age have been collected from adjacent regions, but as yet there has been no mature consideration of this material.

*Chalk Bluffs flora* from the Middle Eocene of California.—MacGinitie's recent study (MacGinitie 1941) indicates that most of this flora represents a lowland-valley forest of subtropical type. Topographic diversity is suggested by the occurrence in the fossil record of upland-temperate genera. Small florules from beds of the same age to the west are interpreted as representing strand vegetation.

*Clarno flora* of Upper Eocene age from the John Day Basin of Oregon (Knowlton 1902), together with the *Comstock* (Sanborn 1935) and other less well known floras from western Oregon.—These floras show the occurrence of an essentially uniform forest across the state, indicating that marine control of climate was not limited during Upper Eocene time, as now, by the Cascade Range. The vegetation was subtropical in aspect, with several florules of more temperate aspect suggesting upland habitats.

*Steel's Crossing* and other floras commonly referred to as the *Puget*, from the Upper Eocene of western Washington (Newberry 1898).—No comprehensive study of these important units has ever been made, but large collections at hand indicate that the Steel's Crossing flora was of a subtropical character. Somewhat smaller average leaf size suggests less favorable living conditions than in Oregon and California. Material from the Bellingham Bay region appears to be older, and to represent more typically subtropical vegetation. Several floras from eastern Washington, such as the Roslyn and Swauk, seem also to be of Eocene age; like those of eastern Oregon, they indicate the absence of any climatic barrier such as the Cascades now afford.

*Goshen flora* from west central Oregon, occurring in beds believed to be Lower Oligocene on the basis of invertebrates, but closely related to Eocene of adjacent areas (Chaney & Sanborn 1933).—This subtropical flora appears to have lived in a valley near sea level, and to have derived most of its members from Central America and adjacent areas. The *La-Porte flora* (Potbury 1935) from northern California represents a similar forest, perhaps living at a higher elevation.

*Weaverville flora* from northwestern California (MacGinitie 1941).—Somewhat younger than the Goshen, this forest appears to have lived at low elevations along swampy streams, in a humid, warm temperate climate. Mingling of temperate with tropical genera suggests an ecotonal relationship with the southward-moving Aretotertiary flora.

#### FACTORS AND EVENTS

Gradual displacement of the temperate to warm temperate Cretaceous floras of the United States by the Neotropical-Tertiary Flora during Eocene time has been considered in detail by Berry for the eastern United States (Berry 1930, pp. 15-16). Such temperate genera as *Acer*, *Betula*, *Cornus*, *Fagus*, *Liriodendron*, *Pinus*, *Salix*, *Sassafras* and *Sequoia* were

present in Cretaceous time in the eastern United States, and most of them ranged northward into Greenland and Alaska; all of them had disappeared from the area occupied by the Wilcox flora by Eocene time when the climate became warmer, and were largely restricted to high northern latitudes<sup>2</sup> as members of the Aretotertiary Flora. In the interior, at the southern end of the Rocky Mountain area, a similar but less pronounced change in climate may be noted, with the incoming of many new subtropical species and an accompanying northward migration of temperate types. Such Upper Cretaceous genera of the Vermejo flora as *Liriodendron*, *Salix* and *Sequoia* were eliminated by Eocene time, and the Raton flora which succeeded the Vermejo contains many more species of the Lauraceae, Leguminosae and Moraceae, represented by larger leaves of more tropical aspect. There is a less noticeable change from Upper Cretaceous to Eocene floras northward along the Rockies. Dorf's recent studies have shown (Dorf 1942, pp. 100-103) that the Laramie, Medicine Bow and Lance floras, in sequence from south to north, show a progressive change from subtropical to warm temperate; the Denver and Fort Union floras, which lived in the same region during Eocene time, are represented by similar climatic types. There is however another factor involved which seems indicative of rising temperatures in this region; whereas the Upper Cretaceous floras appear, from their association with marine invertebrates, to have occupied a lowland, coastal-plain environment, there was no adjacent ocean during Eocene time to moderate temperatures in the area now occupied by the Rocky Mountains. The persistence of warm temperate to subtropical vegetation into the Eocene, in spite of the less favorable geographic and topographic relations, is therefore suggestive of climatic changes like those in the Mississippi embayment, though less extreme. No floras from the Upper Cretaceous of the Pacific Coast states are available for comparison. From the Upper Cretaceous of Vancouver Island are recorded such temperate genera as *Betula*, *Cornus*, *Juglans*, *Liriodendron*, *Populus*, *Salix*, *Sassafras* and *Sequoia*, all of which ranged north into Alaska. None of them are known to have survived into the Eocene in the Puget Sound region, but all are common members of the Kenai floras of Eocene age to the north. There is indicated here, as in the case of the eastern floras, and to a lesser degree those of the interior, an early Tertiary movement northward of warm temperate to subtropical vegetation, and a concentration of temperate vegetation in high latitudes.

The causes of such wide-spread changes in climate cannot here be discussed beyond suggesting that, following the Cretaceous uplifts in the Caribbean region and along the Cordillera, there were submergences in central and northern South America, Central America, Mexico, the Mississippi embayment and the Antilles, with encroachments of the Pacific Ocean

<sup>2</sup> Or to higher altitudes in the eastern United States, though there is little possibility of plants being preserved as fossils in such situations.

eastward from its present shores. In Eurasia there were broad submergences in western Europe and southeastward along the Tethys trough, with an embayment extending northward along the Urals axis. Since increased circulation of ocean currents and of the atmosphere may be expected to have been general throughout the world, and to have extended mild and humid climate northward, it is appropriate to review briefly the evidence for corresponding forest migrations on other continents.

#### THE NEOTROPICAL-TERTIARY FLORA OF THE SOUTHERN HEMISPHERE

Available floras from low American latitudes indicate that tropical climates have prevailed there from Eocene time down to the present. An Eocene flora from Venezuela shows so close a resemblance to the Eocene of the Mississippi embayment as to suggest that the Wilcox and other floras of the southern United States had their origin in South America during the Cretaceous. Migrations in South America from low to middle latitudes are indicated by Eocene floras of Chile and Patagonia (Rio Pichileufu, Concepcion-Arauco), at latitudes ranging from 37 to 45 degrees. Like the Neotropical-Tertiary Flora of the northern hemisphere, this vegetation was made up largely of angiosperms now found nearer the equator; in addition to abundant Lauraceae, certain families now more characteristic of the southern hemisphere, the Apocynaceae, Myrtaceae and Rubiaceae, were well represented. Such conifers as Araucaria and Podocarpus give these floras an aspect as typically southern as the modern vegetation. There is no reliable evidence of the occurrence of Sequoia south of the equator.

#### PALEOTROPICAL-TERTIARY FLORA

In the submerged basin of western Europe, many subtropical floras are known from older Tertiary deposits. One of the best-known of these is the London Clay flora described by Reid and Chandler (1933) from well-preserved fruits and seeds occurring at 50 degrees north latitude. Among numerous angiosperms whose modern equivalents live in the tropical rain-forest of Indo-Malaysia, the record of *Nipa* is one of the most significant. Now confined to tidal flats at low latitudes, this palm has been recorded southeastward from England across Eurasia, along the shore of the Tethys Sea; it was probably along this shore that the London Clay and other floras migrated northward and westerly across India and the Near East to western Europe.<sup>3</sup> The Tethys Sea appears to have interposed a barrier to migration between the northern and southern hemispheres, resulting in Eocene and later differentiation of their vegetation. The Proteaceae and Myrtaceae are two typically southern families recorded largely south of the Tethys trough from Eocene down to modern times; as in South America, the conifers are typical of the southern hemisphere today, including such genera as *Agathis*, *Daerydium*, *Phyllocladus* and *Podocarpus*,

as pointed out by Florin (1940). The Paleotropical-Tertiary Flora of the southern hemisphere is too inadequately known to provide clear evidence of southward migration routes in the Old World migrations in the fossil records of Africa, Australia and New Zealand.

#### SUMMARY OF TROPICAL-TERTIARY FLORAS

The older Tertiary record of these Floras indicates that they spread poleward from the tropics in the Americas and the Old World, reaching a latitude of approximately 50 degrees on the western sides of the northern continents; in the southern hemisphere their migrations are less adequately known, and appear to have been more limited. Gradual emergence, probably combined with changes in the solar constant and other factors not adequately understood, brought a reversal in the trend toward warmer and more humid climate during the Oligocene epoch. During the remainder of the Tertiary period and down to the present, these subtropical forests have been giving way to temperate members of the Arcto-Tertiary Flora in North America and Eurasia, and to those of the Antareto-Tertiary Flora in the southern continents.

#### ARCTO-TERTIARY FLORA

This temperate assemblage has been so fully discussed in print during recent years that only a brief summary will here be included. Wide-spread over high northern latitudes during Eocene time, many of its genera are recorded also from the Cretaceous of Alaska, Greenland and Siberia. In fact the initial appearance of angiosperms in western Greenland, in beds referred to the Lower Cretaceous, has provided the principal evidence supporting the theory of Holarctic origin for flowering plants. The diversity of these earliest-known angiosperms suggests that they may have come into existence in pre-Cretaceous time; if their date of origin goes back to the Jurassic, they could have migrated north from lower latitudes, together with cycads, ferns and conifers which characterized the vegetation widely distributed from the Arctic to the Antarectic during this period.

Analysis of the Arcto-Tertiary Flora of the Eocene indicates that it may be subdivided into typically temperate and boreal units, the latter occurring in northern Siberia and on arctic islands to within eight degrees of the North Pole (Chaney 1940, p. 482-483). The Eocene existence of *Sequoia*, *Taxodium*, *Pinus*, *Picea*, *Carex*, *Salix*, *Betula* and *Corylus* in regions where the polar night lasts for several months has led to wide speculation regarding continental drift and the migration of poles, as well as to suggestions that the plant remains were carried northward by ocean currents. There appears to be no good reason why hardy ecotypes of these genera, many of which now range far north of the arctic circle, should not have lived in Grinnell Land at a time when winter temperatures were moderate; the existence of polar ice-caps during Eocene time is doubtful, and a wholly different regime of air and water circulation may be

<sup>3</sup> This is the Paltavian flora of Kryzhtofovich (1929, p. 309).



expected to have characterized high latitudes. Recent discovery by Wan-Chun Cheng of a living relative of *Sequoia* in central China, a tree which sheds its leafy twigs during the winter, provides a possible basis for explaining the occurrence of this now warm temperate plant in Grinnell Land. For without leaves, *Sequoia* and *Taxodium* might both be expected to survive a dark winter which was not cold. Occurrence of fossil remains resembling this living Chinese tree, assigned to the genus *Metasequoia* in a paper by Cheng and Hu not yet printed, has been reported from Eocene deposits of Greenland, Spitzbergen and Alaska, and probably in the Cretaceous of Greenland (Lesquereux 1878).

The typically temperate part of the Aretotertiary Flora includes a long list of angiosperms and gymnosperms of which the more common and widely distributed are: *Acer*, *Alnus*, *Betula*, *Carpinus*, *Castanea*, *Cercidiphyllum*, *Cornus*, *Crataegus*, *Fagus*, *Fraxinus*, *Ginkgo*, *Juglans*, *Pinus*, *Platanus*, *Populus*, *Quercus*, *Salix*, *Sequoia*, *Taxodium*, *Tilia*, *Ulmus* and *Zelkova* (Hollick 1936). All of these genera except *Carpinus*, *Castanea*, *Cornus*, *Crataegus*, *Fagus*, *Fraxinus*, *Salix*, *Zelkova* had become established at high latitudes during later Cretaceous time, suggesting that the Aretotertiary Flora was largely derived from an Aretotertiary Flora. Similarity in composition of the Aretotertiary Flora from Alaska to Greenland, Spitzbergen and Siberia confirms geologic evidence of more extensive and continuous land masses around the North Pole.

On the southern margin of the area occupied by this temperate forest, which was largely made up of deciduous trees, there appear other genera whose modern members live under warmer conditions. A Kenai florule from Kupreanof Island, at latitude 57 degrees north in southeastern Alaska, includes such temperate genera as *Castanea*, *Juglans*, *Populus*, *Quercus*, *Sequoia* and *Ulmus*, together with several Neotropical-Tertiary genera, *Ceratophyllum*, *Dillenia*, *Dioon*, *Laurus*,<sup>4</sup> *Magnolia*, *Malapouma*, *Pterospermum*. Older Tertiary floras from southern British Columbia, Alberta and Saskatchewan, at latitude 51 degrees north, contain warm temperate to subtropical genera such as *Aralia*, *Catalpa*, *Cinnamomum*, *Ficus*, *Laurophyllum*, *Magnolia* and *Pterospermum*, although their dominant genera are typically temperate members of the Aretotertiary Flora. Such an ecological relationship with the Neotropical-Tertiary Flora to the south has already been pointed out in the case of the Fort Union flora, which includes numerous temperate genera of the Aretotertiary Flora. Similar ecotones may be noted in older Tertiary floras of central Europe at latitudes 48-50 degrees north, and of Manchuria at latitude 42 degrees north.

With the trend toward a cooler and less humid climate, which became pronounced at the end of the Oligocene epoch, the Aretotertiary Flora migrated southward from Alaska. Reference may be made to the possibility, already mentioned, that some members of the temperate forest of the Cretaceous low-

lands may have shifted up-slope and survived at higher altitudes in the United States during the Eocene. In that event they would have been in a position to have migrated down-slope during middle Tertiary time with the return of temperate climate to the lowlands. Floras of later Tertiary age in Oregon and elsewhere at middle latitudes disclose the elimination of various species and even genera during this journey, which occupied ten million years or more; other genera were added, changing the composition of the Flora as known from the Eocene of Alaska. But in its general aspect, the Bridge Creek flora from the John Day Basin of Oregon (Chaney 1925), and the Miocene floras which came after it in the western United States, show essentially the same type of vegetation as the Alaska Eocene, requiring a summer-wet climate, a moderate annual range in temperature, and a valley environment. In some of the larger valleys extending in from the coast, such floras as the Latah (Knowlton 1926) and Mascall (Chaney 1925) maintained a minor relic element of the Neotropical-Tertiary Flora, including such genera as *Cedrela*, *Gordonia*, *Laurus*, *Machilus*, *Magnolia*, *Oreopanax*, and *Tetracera*. Along the coastal plain at the mouths of these valleys, *Sabal*, *Catalpa*, *Ocotea* and *Persea* appear to have been common, with temperate trees such as *Alnus*, *Platanus* and *Sequoia* largely restricted to adjacent hills. Largely as a result of the removal of continental deposits during Pleistocene glaciation, the later Tertiary floras of eastern North America are incompletely known. Small floras from New Jersey to Maryland (Berry 1916b) indicate the Miocene occurrence of such Aretotertiary genera as *Carpinus*, *Platanus*, *Pinus*, *Quercus*, *Salix* and *Ulmus*, with *Ficus* and other Neotropical-Tertiary leaves in a marked minority. The Miocene Shanwang flora of northern China (Hu & Chaney 1938-1940), and many of the later Tertiary floras of central and western Europe, show mixtures of their dominant Aretotertiary constituents with residual genera from the retreating Neotropical Flora. This sort of mingling continued even into the Pliocene in Europe, where broad submergence was maintained nearly to the end of the Tertiary period.

To some extent in Europe, and to a marked degree in most other parts of the northern hemisphere, the cool, dry climate of the Pliocene brought further shifting of the Aretotertiary Flora coastward and southward. A regime of dry summer climate in western North America resulted in the disappearance of many broad-leaved, deciduous genera such as *Carpinus*, *Fagus*, *Tilia*, and later, *Ulmus*; all of these have survived in the eastern United States where rain falls during the summer. The redwood was restricted to western Oregon by the rising Cascade Range, which in the Pliocene, as now, cast its rain shadow over the John Day Basin and other regions in eastern Oregon (Chaney 1944). Along the coast of central California, the Upper Pliocene Sonoma flora is largely made up of Aretotertiary species (Axelrod 1944), but a short distance into the in-

<sup>4</sup> Probably *Persea*.

terior these give way to the Madro-Tertiary Flora as discussed below. From causes not readily defined, but probably having to do with limited summer rainfall on the Pacific Coast, *Cercidiphyllum*, *Ginkgo*, *Trapa*, *Zelkova* and other genera were eliminated from North America altogether by the close of the epoch, although they have survived at corresponding latitudes on the western side of the Pacific. A small flora from the Citronelle formation of the Gulf states (Berry 1916c) closely resembles the existing forest of the coastal plain, with only limited representation of Asiatic and tropical forms. By the end of the Tertiary period the generalized forest which migrated south from Alaska had taken on modern regional characters in western and eastern North America; the Neotropical-Tertiary Flora had been restricted to latitudes some 20 degrees south of its Eocene occurrence. Similar southward migrations are indicated by the later Tertiary distribution of Arcto- and Neotropical-Tertiary Floras in Eurasia (Hu & Chaney 1938-40, pp. 103-117).

#### THE ANTARCTO-TERTIARY FLORA

Corresponding equatorward movements of the vegetation of the southern hemisphere may be noted briefly. Uplift of the Andes to their present height during the Pliocene and Pleistocene epochs, together with the general changes in climate noted to the north, appear to have been responsible for the shifting northward of the Neotropical-Tertiary Flora from Chile and Patagonia to Brazil, and for migration of the Antarcto-Tertiary Flora from high to middle southern latitudes. In his excellent paper on fossil conifers of south Chile (Florin 1940), Florin has summarized the records of temperate plants, angiosperms as well as conifers, at high southern latitudes during the Eocene; his opinion that the vegetation of the southern and northern hemispheres developed independently throughout the Tertiary period seems wholly confirmed by the evidence he presents. Such conifers as *Aemopyle*, *Araucaria* and *Podocarpus*, angiosperms as *Knightia*, *Laurelia* and *Nothofagus*, appear to have been largely or wholly southern in their Tertiary distribution as they are today. Their migration northward from Antarctica and the southern tip of South America, where they are recorded in Eocene rocks, to their present area of occurrence in south temperate latitudes, and in the case of the conifers into the tropics, appears to correspond closely to the southward movement of the Arcto-Tertiary Flora which occurred at the same time.

#### THE MADRO-TERTIARY FLORA

In our discussion of Pliocene floras, reference has been made to the wide extent of plants whose affinities are with those now living in dry regions. Axelrod has suggested that many of these had their center of origin in the Sierra Madre of northern Mexico, and that during the Tertiary they migrated northward along arid ranges, spreading out to the east and west in response to the trend toward reduced precipitation in the continental interior. It is possible that

vegetation at middle latitudes in the United States may have received increments of this Madro-Tertiary Flora as early as Eocene time, for the Green River flora contains several plants, including the oldest known cactus, *Eopuntia*, which suggest a dry southern source. During the Oligocene epoch a northward movement from northern Mexico is recorded by the presence of ten or more Sierra Madrean species in the Florissant flora of Colorado, a flora otherwise Arcto-Tertiary in composition. By Middle Miocene time, the Madro-Tertiary Flora was well established in the interior of southern California; here the Tehachapi (Axelrod 1939) and Mint Canyon (Axelrod 1940) floras show a strong development of the Southwest American Element, with small-leaved oaks and numerous other genera which make up an important part of the existing chaparral formation. Axelrod's maps of later Tertiary distribution of the Madro-Tertiary Flora (Axelrod 1939, p. 59) indicate Miocene extensions of a few of these southern forms into Washington and Idaho before the close of the epoch. At the end of the Miocene, when the East American and East Asian Elements were losing many of their members in the interior of western North America, apparently as a result of reduced summer rainfall, these hardy, drought-resistant plants from northern Mexico were moving northeastward into Texas and Oklahoma (Chaney & Elias 1936), and were becoming established on the western slopes of the central Sierra Nevada (Condit 1944). By Middle Pliocene time the Madro-Tertiary was the dominant Flora of the lowlands nearly to the coast. The Mulholland flora is an example of the oak savanna vegetation in the Coast Ranges east of San Francisco Bay (Axelrod 1944); only a few Arcto-Tertiary species had survived in it. As already mentioned, the somewhat younger Sonoma flora from the adjacent coast is largely made up of Arcto-Tertiary genera, although it also includes a few species of Madro-Tertiary origin.

#### SUMMARY

The fossil record during the Tertiary period, representing approximately sixty million years of earth history preceding the period in which we live, indicates progressively more temperate types of vegetation at middle and high latitudes both in the northern and the southern hemisphere; there is no evidence of marked change at low latitudes. The following major units of vegetation in North America have been considered:

*The Neotropical-Tertiary Flora* ranged northward to latitude 49 degrees on the west side of the continent during Eocene time, and is recorded to progressively more southerly latitudes eastward across the continent, reaching only as far north as latitude 37 degrees in the Mississippi embayment of the southern United States. During the Oligocene and Miocene epochs it was restricted southward in western North America to central and southern California, leaving relicts to the north along the Oregon coast; by Plio-

cene time only a few remained north of the Mexican border. In the eastern United States, most of the warm temperate and subtropical species had been eliminated by Miocene time. The Neotropical-Tertiary Flora has survived in the Antilles, northern South America, Central America and Mexico; numerous relicts occur in southern Florida and sparsely to the north, where their habit is largely as shrubs and vines. Several subtropical families are similarly represented in the living vegetation of western North America. In the southern hemisphere there was a northward shift of the Neotropical-Tertiary Flora from middle to low latitudes during the Tertiary period, and corresponding equatorward movements are indicated by the Paleotropical-Tertiary Flora.

The Arcto-Tertiary Flora ranged northward to latitude 67 degrees in Alaska during Eocene time, with a boreal unit extending to within 8 degrees of the North Pole; its occurrence at high latitudes east of Great Bear River is unknown, for Tertiary deposits have been completely removed from most of Canada by Pleistocene glaciation. During the Oligocene epoch it is recorded from Washington and Oregon, and had reached central California by the end of the Miocene; in the Rocky Mountain area, this temperate Flora extended into Colorado in Oligocene time, and in the eastern United States it was well established as far south as Maryland during the Miocene. Occurring as a relatively uniform forest throughout much of the northern hemisphere as late as Miocene time, this Flora shows evidence of regional diversity during the Pliocene epoch. Various genera disappeared from western and eastern North America, largely as a result it may be supposed, of a changing regime of summer rainfall and of seasonal temperatures; other genera were eliminated from the whole of this continent, and have survived only in Eurasia. The Arcto-Tertiary Flora has survived in North America at middle latitudes in two main provinces, an eastern characterized by broad-leaved, deciduous trees, and a western characterized by conifers, broad-leaved evergreens, and broad-leaved deciduous trees and shrubs. Many details concerning the history, distribution and composition of the living forests of the eastern province have been presented by Braun, while similar material for western vegetation has been assembled by Mason and Axelrod.

The Madro-Tertiary Flora ranged northward from northern Mexico during the Tertiary period whenever favorable climatic, and wherever favorable topographic, conditions existed. It reached its widest distribution in the western United States during the Pliocene epoch, and while it is now largely confined as a dominant to the southwestern interior and adjacent Mexico, it is still represented over a much larger area in the West.

The existence of broad areas of later Tertiary grasslands has long been predicated by vertebrate paleontologists on the basis of the structures of fossil mammals. The plant record has been singularly lacking in the remains of prairie grasses until the

discovery of fossil grass hulls by Elias in 1931 (1942). Since that time numerous well preserved remains, largely of the tribes Stipeae and the Paniceae, have been collected by Elias in deposits of Miocene and Pliocene age on the High Plains. The expansion of grasslands during later Tertiary time was a natural consequence of the trend toward arid climate with widely ranging temperature, a trend indicated by changes in forest composition as above described. There is little direct evidence as to the place of origin of these prairie grasses; doubtless some of them developed at the north, migrating southward on the borders of the Arcto-Tertiary Flora; others may have come up from northern Mexico with the Madro-Tertiary Flora.

While the three major units of Tertiary vegetation have developed ecotones, extending both along latitudinal and altitudinal boundaries, from the Eocene down to the present in North America, there are evidences of progressive differentiation between them and the corresponding floristic units of other continents. Until the Pleistocene or late Tertiary break in the Bering land bridge, at least the northern part of the Arcto-Tertiary Flora was co-extensive from Eurasia to North America, and the forests of northeastern Asia still show many resemblances to those of our continent. For the more southerly members of the Flora, a climatic barrier has existed since Miocene time, and numerous minor differences in composition have developed between the two continents; one of the most striking of these is the absence from the Tertiary and modern floras of Eurasia of the black oaks (sub-genus *Erythrobalanus*) which first appeared abundantly in the Miocene record of the United States; by this time the climate in Alaska appears to have been too cold to permit migration of the black oaks across the Bering land bridge. The Arcto-Tertiary Flora shows almost nothing in common with the Antareto-Tertiary, from which it has been separated at least since Cretaceous time. The Neotropical-Tertiary Flora of the northern hemisphere shows little resemblance to the Paleotropical-Tertiary Flora of Eurasia, from which it must have been separated by a climatic, as well as topographic, barrier throughout Cenozoic time (Chaney 1940, pp. 481-486). The Neotropical-Tertiary Flora of North America also differs to a marked degree from that of South America, as does the Paleotropical-Tertiary Flora on either side of the equator in the Old World; the topographic barriers of the Caribbean and Tethys seaways appear to be responsible for these major differences in composition from the northern to the southern hemispheres during Tertiary time.

The distribution and composition of Tertiary floras in North America and elsewhere in the world make possible the following conclusions:

(1) Continental platforms and ocean basins have occupied essentially their present relative positions at least since the wide-spread emergence which brought the Cretaceous period to a close.

(2) During the Tertiary period and down to the present, in all parts of the world outside the tropics,

major modifications in floral composition at given latitudes have been controlled by climatic changes. Since Eocene time, a trend toward lower, more variable temperatures, and toward reduced and more seasonal precipitation, has provided the major incentive to forest migrations.

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EVIDENCE ON RATES OF EVOLUTION FROM THE DISTRIBUTION OF  
EXISTING AND FOSSIL PLANT SPECIES

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IN A SYMPOSIUM ON  
ORIGIN AND DEVELOPMENT OF NATURAL FLORISTIC AREAS  
WITH SPECIAL REFERENCE TO NORTH AMERICA



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# EVIDENCE ON RATES OF EVOLUTION FROM THE DISTRIBUTION OF EXISTING AND FOSSIL PLANT SPECIES

## INTRODUCTION

In order to understand the origin of natural floristic areas and the plant associations found in them, we must know something about the rates at which plant species can evolve, and of some of the factors which determine these rates. The ideal way to obtain such information would be from the direct evidence provided by the fossil record. But this record is too imperfect for us to be able to rely on it entirely for our information on rates of evolution in the Angiosperms. To be sure, the number of geological horizons and geographical localities in which fossil Angiosperms have been found is now large, and is being steadily increased. But the remains found in these localities, since they consist mostly of leaves, can give us for the most part only two types of information. In the first place, they can tell us with some accuracy what was the nature of the woody flora of the locality at the time of deposition of the fossils; whether it was temperate or tropical, mesophytic or xerophytic, etc. And secondly, we can learn from the fossil record the approximate age and past distribution of modern genera and species of woody plants. On the other hand, the very nature of this record makes difficult the identification of the morphologically different ancestors of modern species and genera, and the determination of the time when they existed. In other words, if we find as fossils leaves and particularly fruits resembling those of modern species and genera, we can safely make inferences concerning the age and past distribution of these

groups. But if a species or genus is absent from the known record, we cannot infer that it did not exist. And in very few examples are there series of fossil types which enable us to trace out the course and rate of evolution of any species or genus. We can learn from the fossil record of Angiosperms much about evolutionary conservatism and stability, but this record tells us relatively little about evolutionary progress.

Although the fossil evidence is being discussed in detail in this symposium by Dr. Chaney, I shall, nevertheless, present two examples which typify the nature of this evidence and will serve as a basis for comparing it with the other types of evidence to be discussed. One is the genus *Fothergilla*, a shrub of the Hamamelidaceae, which has at present a disjunct distribution in the northern temperate zone, namely in the southeastern United States and in Afghanistan. This distribution, as Fernald (1931) has pointed out, marks it as a relic of the formerly widespread Arcto-Tertiary forest, but is anomalous in that *Fothergilla* is now unknown from eastern Asia, the largest repository of Tertiary relics in the world. Of particular significance, therefore, is the discovery by Hu and Chaney (1940) of leaves identical with the modern American *F. Gardeni* in a flora of Miocene age in Shantung Province, China. Since in other respects this Miocene flora is closely similar to the modern flora of temperate western China, we can infer that extinction of a particular species from an area can be effected even though the flora as a whole is relatively little altered.

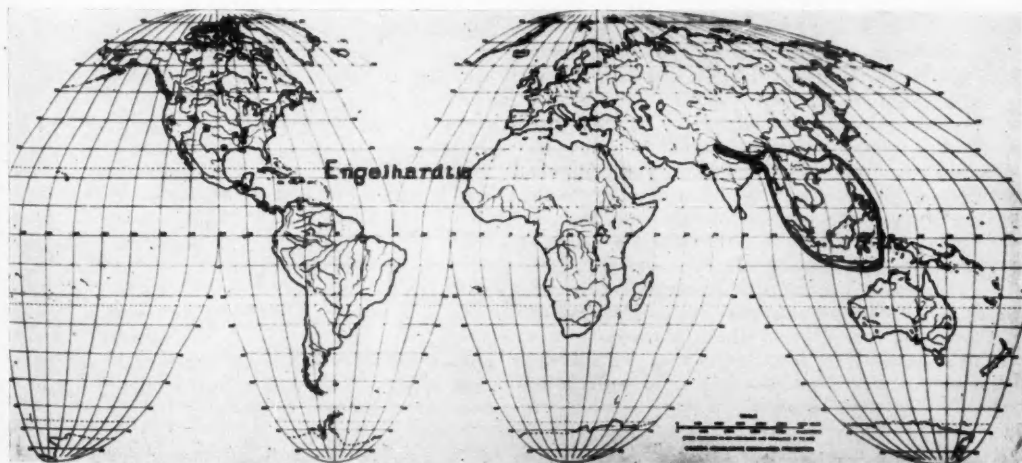


FIG. 1. Present distribution of the genus *Engelhardtia* in Asia (solid line) and Central America (solid circles), and location of fossil records for this genus in North America (solid squares).

The second example is the genus *Engelhardtia*, of the family Juglandaceae, selected because its present distribution is subtropical and tropical, and because its very characteristic fruits have been found in a number of fossil localities. At present *Engelhardtia* occurs chiefly in southeastern Asia and adjacent Malaya, but it is found also in a few restricted localities of Mexico and Central America (Fig. 1). Fossil fruits of this genus have long been known from the early Tertiary deposits of Europe, and have been found more recently in various parts of the United States, where they are confined to deposits of Eocene age. Perhaps the most extensive remains of *Engelhardtia* are those from the Sierra Nevada of California (MacGinitie 1941) where they are among the commonest of the Eocene fossils. Although fruits of this genus are not known from farther north than Idaho, leaves which may belong to it have been found in the Kenai formation of Alaska (Hollick 1936), indicating an early Tertiary distribution far north of the present one, and suggesting how *Engelhardtia* and other genera with a similar modern distribution migrated from the Old World to the New.

The fossil record, because of its very nature, can tell us about the past occurrence of only certain types of plants, and these are almost entirely the larger woody elements of a flora. Nevertheless, it has confirmed to such an extent the concepts which discerning plant geographers have developed about the past occurrence and distribution of modern species that we can now with greater confidence than ever make inferences from the patterns of distribution which we find today. And this is particularly true of herbaceous species which have distribution patterns similar to those of woody species known from the fossil record. Many such patterns are known, but the largest group is that confined to the temperate forests of eastern North America and eastern Asia. The great age of the groups with this distribution pattern was postulated long ago by Asa Gray, and has been reaffirmed by many recent works (Fernald 1929, 1931). And the increasing number of records from early and mid-Tertiary deposits shows that close relatives of these species were widespread at periods of fifteen to forty million years ago.

This makes particularly significant the fact that among the herbaceous groups now confined to eastern America and eastern Asia there are representatives not only of families generally regarded as primitive, like the Ranunculaceae, Berberidaceae, and Liliaceae, but also of advanced families like the Orchidaceae, Polygonaceae, and Gramineae. Four such examples are *Cypripedium arietinum*, *Polygonum sagittatum*, *Tovara virginica*, and *Brachyelytrum erectum* (Fernald 1929, Stebbins 1942a). In all of these, the species are identical on the two continents, and the populations are at most variably or subspecifically distinct. These advanced herbs, therefore, are not only ancient; they have evolved very little during the past several million years. And among them is an annual, *Polygonum sagittatum*, which has therefore gone through millions of generations without

progressive evolution. In fact, we can safely make the generalization that within the Aretotertiary forest the evolution of the herbaceous elements of the flora has been as slow as that of the woody species.

### ALLOPOLYPLOIDS AND EVOLUTION

The interpretation of patterns of distribution of modern species which do not belong to plant associations well represented in the fossil record is much more difficult, but in many cases safe inferences can be made. And in certain instances cytogenetic evidence has greatly aided such inferences. It is now a well established fact that a large proportion of species of the higher plants have originated through allopolyploidy, that is through hybridization between two preexisting species and consequent doubling of the chromosome number in the sterile hybrid. And the origin of some of these allopolyploids, such as *Galeopsis Tetrahit* (Muntzing 1931), *Nicotiana tabacum* (Goodspeed and Clausen 1928; Greenleaf 1941), and *Triticum aestivum* (McFadden and Sears 1946), as been demonstrated by the artificial synthesis of the species or a closely related form. And in many other examples the probable parents of a natural allopolyploid have been inferred from strong morphological and cytological evidence.

If the two species known or postulated on good evidence to be the parents of an allopolyploid still occur together and have a chance to hybridize, the likelihood is that the species is of recent origin, and arose in the region where the two ancestral species now occur together. Such is the case with *Pentstemon neotericus* Keck (Clausen 1931) and *Madia citrigracilis* (Clausen Keck and Hiesey 1945). But if these parental or ancestral species now occur in areas more or less widely separated from each other, then we must conclude that the allopolyploid has existed as a stabilized species for a long period of time, and that it originated under conditions which permitted a different distribution of species from that which now prevails. And by study of the distribution of significant fossil species, supplemented by what is known of past climates, the time and conditions under which the ancestral species met to produce the allopolyploid can often be inferred. The potential use of allopolyploids in plant geography was pointed out by the writer a few years ago (Stebbins 1942b), and since then a number of examples have been developed which have demonstrated even better these potentialities.

The first series of examples are allopolyploids which probably originated in the Pleistocene epoch. Of these the best known and most clearly authenticated is *Iris versicolor* (Anderson 1936). Its parental species, *I. setosa* var. *interior* and *I. virginica* var. *Shrevei*, are now found respectively in central Alaska and the Mississippi Valley-Great Lakes region. The present distribution of *I. versicolor* indicates that it originated in the latter area, and since it is found almost entirely within the territory covered by the Wisconsin ice, it probably originated during the Pleistocene epoch. Anderson has therefore made the logical inference that during this time *I. setosa*



var. *interior* existed in the northeastern United States, probably along the moraine of the retreating ice. A very similar pattern of distribution is that of *Oxycoctus* (Camp 1944). In this case the likelihood is also that the tetraploid *O. quadripetalus* Gilib. originated during the Pleistocene epoch, and that the diploid *O. microcarpus* Turcz., now confined to northwestern North America and Eurasia, was at that time distributed along the southern margin of the glaciers, where it came into contact with the southern diploid, *O. macrocarpus* (Ait.) Pers. These examples point to the same direction, and suggest that a considerable element of the flora now confined to the Rocky Mountain region or Alaska may have existed during the Pleistocene epoch along the southeastern margin of the ice sheet.

A still older group of allopolyploids is that of *Bromus* subg. *Ceratochloa*. The North American species of this subgenus *B. carinatus*, *B. marginatus*, and others, are chiefly octoploids which contain four different haploid genomes. Three of these genomes are homologous to and derived from those found in the hexaploid species of the subgenus *Ceratochloa* endemic to South America (Stebbins and Tobgy 1944). A hybrid recently produced by the writer between *B. marginatus* and the diploid *B. laevipes*, native to California, has shown that the fourth genome in *B. marginatus* and *B. carinatus* is homologous with those of the diploid species of the subg. *Bromopsis* endemic to North America (Fig. 2). Thus the most likely origin of these octoploid *Bromus* species is through hybridization and allopolyploidy involving the ancestors of the present North American species of the

subg. *Bromopsis* and the progenitors of the now South American species of subg. *Ceratochloa*. Since the octoploids almost certainly arose in North America, we must postulate that in some earlier geological epoch hexaploids similar to these South American species existed on this continent.

A clue to the time when this could have occurred is provided by the studies of Elias (1942) on the fossil grass fruits belonging to the tribe Stipeae which he has found in the Miocene and Pliocene deposits of the North American Great Plains. He refers these to two extinct genera, *Stipidium* and *Beriochloa*, on the basis of an inference. Because no remains of awns have been found with the fruits, he has inferred that they had weak, non-indurated awns, in contrast to the firm, indurated awns possessed by the modern species of *Stipa* and *Piptochaetium*, which in other respects the fossil fruits closely resemble. The weakness of this inference, however, lies in the fact that the awns of the modern species become separated from the fruits after they have been even a short while in the ground, and are easily broken in pieces by a small amount of mechanical injury. Such awn fragments might be carried by stream currents away from the site of deposition of the fruits, or might be so broken up and distorted as to be unrecognizable. An equally valid inference that these fossil fruits possessed strong awns may be made on the following grounds. All of them possess long, sharp callus points on their bases, a characteristic which in all modern species of grasses is associated with the presence of strong awns. This is because the awn-callus combination serves as a drill, burying the fruits deep in the ground, and insuring their germination even under relatively dry conditions. Awns may often have some function without the presence of calli, but an elongated, sharp-pointed callus without an accompanying awn not only is unknown in all the multitude of grass species, but also has no reason for existing. Its past occurrence in species otherwise almost identical with modern ones is therefore highly unlikely.

If, therefore, we disregard this inference about the character of the awns, and compare the fossil fruits with their nearest modern counterparts, we find certain striking resemblances, not to present day species of the Great Plains, but to certain species of the temperate South American pampas. All of these modern species have been recently placed by Parodi (1944) in the genus *Piptochaetium*, subgenus *Podopogon*. The resemblances between the fossil North American and the contemporary South American fruits are shown in Figure 3. Types with slender lemmas referred by Elias to the genus *Stipidium* are represented by the modern *P. Hackelianum* (Areeh.) Parodi, *P. napostaense* (Speg.) Hackel, and *P. Cabrerae* Parodi, while the fossil "genus" *Beriochloa* contains mid-Pliocene forms similar to the modern *P. bicolor* (Vahl.) E. Desv. Intermediate types of fruits are represented in the fossil record by *Stipidium intermedium* and *S. variegatum*, and among modern species by *Piptochaetium Ruprechtianum* E.



FIG. 2. Distribution of the diploid species of *Bromus*, subg. *Bromopsis*, in North America, of the hexaploid species of subg. *Ceratochloa* in South America, and of the derived allo-octoploid species of subg. *Ceratochloa* in North and South America.

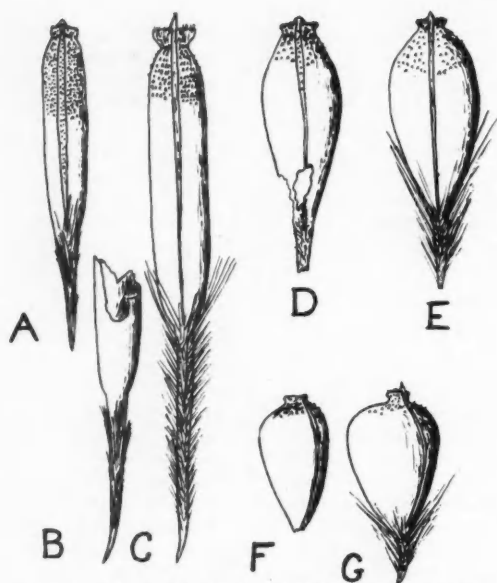


FIG. 3. Fruits of fossil *Stipidium* and *Berriochloa*, and of living *Piptochaetium*. A and B, *Stipidium commune* Elias, redrawn from Elias, 1942, plate 9, Figures 3 and 4. C, *Piptochaetium napostaense* (Speg.), Hackel, from Villa Mercedes, Prov. San Luis, Argentina, Covas 1071. D, *Stipidium intermedium* Elias, from Elias, 1942, plate 11, fig. 10. E, *Piptochaetium Ruprechtianum* Desv. from Tandil, Prov. Buenos Aires, Argentina, Cabrera 6871. F, *Berriochloa amphoralis* Elias, from Elias, 1942, plate 13, fig. 1. G, *Piptochaetium bicolor* (Vahl.) Desv., from Sierra de la Ventana, Prov. Buenos Aires, Argentina, Cabrera 5761.

Desv. A noteworthy fact is that only the most recent, mid-Pliocene species of the fossil series resemble the modern ones. The older species, and particularly those of the Miocene period, have no counterparts among modern species anywhere.

Furthermore, a number of South American species of *Piptochaetium*, including *P. bicolor*, have been found by Dr. J. I. Valencia (unpubl.) to have the haploid chromosome number  $n=11$ . On the other hand, their contemporary North American relatives, including both *P. fimbriatum* of New Mexico and *Stipa comata* and *S. spartea*, may well be allopolyploids which have for one parent one of the "Stipidium" species of the Pliocene flora.

Returning to the genus *Bromus*, we can say that two of the *Ceratochloa* species with 21 pairs, *B. catharticus* (Vahl.) and *B. Haenkeanus* Presl., have much the same distribution in South America as modern *Piptochaetium* species, and so by direct inference may be presumed to have existed in North America during the Pliocene epoch along with the species of *Stipeae* described by Elias. This, then, is the most likely time of origin of the octoploids, and in this example the evidence from fossils and that from modern polyploids supplement each other very well.

The next group of allopolyploids whose origin has been inferred on good evidence is in the genus *Oryzopsis* (Johnson 1945). Two common woodland species of eastern North America, *O. racemosa* and *O. asperifolia*, both have 23 pairs of chromosomes. They are morphologically intermediate between North American species of the subgenus *Euoryzopsis* with 11 pairs (*O. pungens*, *O. micrantha*, *O. exigua*) and Eurasian species of the subgenus *Piptatherum* with 12 pairs, particularly *O. holciformis*, *O. Munroi*, and their relatives (Fig. 4). The latter are associated in the eastern part of their range with the warmer, drier elements of the deciduous forest, although farther west they are even more xerophytic in their habitat preferences. The restriction of the polyploids to

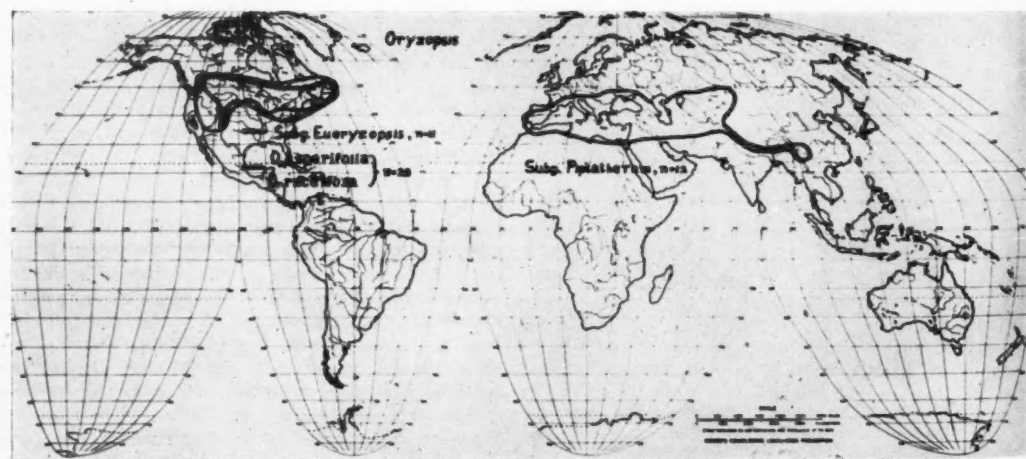


FIG. 4. Distribution of *Oryzopsis*, subgenus *Piptatherum* ( $n=12$ ) in the Old World, and of the diploid ( $n=11$ ) and polyploid ( $n=23$ ) species of subgenus *Euoryzopsis* in North America.

North America suggests again that they originated on this continent, where their 12-paired ancestors, now restricted to Eurasia, must once have existed. In this connection we can note that many of the early and mid-Tertiary floras of western North America contain relatives of species now confined to temperate eastern Asia, along with the counterparts of many eastern American species (Chaney 1940). In conjunction with this mixed forest, therefore, the two groups ancestral to the modern *Oryzopsis* polyploids may have met and hybridized. Since the Asiatic element disappeared from the western American floras during the Miocene, the age of *O. asperifolia* and *O. racemosa* is probably not less than the middle of that epoch.

A group of allopolyploids which may be even older is that of the New World tetraploid species of *Gossypium*, from which the cultivated cottons have been derived. Experimental evidence (Skovsted 1934; Beasley 1942) has shown that the ancestors of these allotetraploids are on the one hand diploid Old World species similar to the Asiatic *G. arboreum* L. and on the other New World diploids of which the closest modern relative is *G. Raimondii* Ulbr. of Peru. Two hypotheses have been offered as to the time when the hybridization and allopolyploidy occurred. Hutchinson and Stephens consider that *G. arboreum* was brought to America by Polynesian or other pre-Columbian immigrants in recent prehistoric times, and that the allopolyploids originated in cultivation. All of the spontaneous occurrences of tetraploid *Gossypium* species are believed to be escapes from cultivation. Harland (1935), on the other hand, believes that these tetraploids originated in early Tertiary or Cretaceous time, and that the connection between the Asiatic and the American diploids was via a land bridge across the Pacific Ocean, including the islands of Polynesia.

Against Hutchinson's hypothesis are the existence of undoubtedly wild tetraploid species of *Gossypium* on the coast of Ecuador, the Galapagos Islands, and Hawaii. The writer has been assured by Dr. Harold St. John and Dr. Otto Degener, both of whom have had a wide experience with the Hawaiian flora, that *G. tomentosum* Nutt. is almost certainly native on these islands. It occurs entirely with other native species, and is not used by the aborigines. Its lint is too short for any practical purpose. Dr. H. K. Svenson, in his thorough study of the plant associations of the coast of Ecuador (1946), has noted a species of *Gossypium* similar to or identical with the tetraploid *G. Darwinii* of the Galapagos, and has assured the writer that both of these occur in natural plant associations. In contrast to *G. peruvianum*, and other South American tetraploids, their fibre is worthless, and they are not used by the aborigines. There is strong evidence, therefore, to support the opinion of Kearney (1942), that strictly wild tetraploid species of cotton occur which must have existed before the advent of man.

We must therefore accept as much more probable that part of Harland's hypothesis which sets an early

date for the origin of the New World tetraploid cottons. But in the light of the paleontological evidence discussed above (Chaney 1947) and exemplified by the early Tertiary distribution of *Engelhardtia*, the assumption of a migration across the Pacific is unnecessary. The subtropical woody flora characteristic of the Eocene deposits of the United States contains a mixture of Asiatic and New World elements, so that it is highly probable that a similar mixture was found among the herbaceous species, including *Gossypium*. The most likely hypothesis, therefore, is that hybridization between relatives of *G. arboreum* and the New World diploids took place in North America in the early part of the Tertiary period, and that the allopolyploids spread southward from this center, as well as out onto the Pacific Islands. With the cooling of the climate in the middle of the Tertiary period, all except certain of the New World diploids disappeared from North America, but the tetraploids survived in South America and perhaps also on the West Indies. If this hypothesis is correct, then the tetraploid cottons, with an age of anywhere from forty to sixty million years, are the oldest polyploids about which we have any evidence. Further cytological exploration of the tropical floras of the New World may uncover other similar examples, which would be one of the best ways of strengthening the case for the age of *Gossypium*.

Two types of inferences can be drawn from the examples given above. In addition to inferring that the ancestors of each allopolyploid had at some particular past epoch of time a different distribution from their present one, we must also conclude that at the time when they gave rise to the polyploid, these ancestors were as well differentiated from each other as at present. Thus the differentiation of species on the diploid level probably took place in *Gossypium* before the end of the Eocene epoch, of subgenera in *Oryzopsis* before the Miocene, of subgenera in *Bromus* and *Piptochaetium* before the middle of the Pliocene, and of species in *Oxycoecus* and *Iris* before the Pleistocene. In *Madia* and *Pentstemon*, species differentiation on the diploid level may be recent and still taking place.

#### SPECIES CLUSTERS AND RAPID EVOLUTION

The evidence just cited from paleobotany and from distribution provides us with good examples of evolutionary stability, but since it fails to give us a good picture of plants which differed from and were the forerunners of modern species, we cannot rely on it for information about rapid evolutionary progress. The best evidence for rapid evolution in the higher plants comes from a different type of distribution pattern, namely the presence in a restricted area of clusters of closely related species, particularly if the region concerned is one which is known to have undergone many climatic and edaphic changes in recent years. This was pointed out some time ago by Sinnot (1916), who cited the southwestern United States as such a region. Careful taxonomic and cytogenetic studies of some of these species clusters in California

has fully borne out this point of view. Particularly noteworthy is the tribe Madinae of the family Compositae, in which species relationships and speciation processes have been fully analyzed by the largely unpublished work of Clausen, Keck, and Hiesey (1941). In this tribe there are many examples of closely related species which occupy localities near together but nevertheless geographically and ecologically distinct, and which are separated from each other by imperfectly developed genetic isolating mechanisms. Typical examples are *Layia Munzii*, *Jonesii*, and *leucopappa*, *Layia gallardoides* and *L. hieracioides*, and the *Hemizonia congesta* complex. These species all occur in the Coast Ranges, which during the Pleistocene epoch have seen the retreat of seas, the opening of valley floors to colonization by land plants, the uplift by faulting of mountain ridges, with the consequent formation of "rain shadows," and the alternation between pluvial and dry periods coincident with the advance and retreat of the ice sheet farther north. And in at least some cases the habitats which they occupy have been made available by these secular changes. This pattern found in the Madinae is undoubtedly repeated with variations in most of the genera of winter and spring annuals in the families Cruciferae, Leguminosae, Polemoniaceae, Hydrophyllaceae, Boraginaceae, and Scrophulariaceae which are so rich in species in these Coast Range foothills. And although, as one might expect, the number of perennial species groups which show evidence of this recent diversification is smaller, there are nevertheless excellent examples in *Delphinium* (Lewis and Epling 1946), *Brodiaea* (Burbank 1944), and *Calochortus* (Ownbey 1940), while even in woody genera, like *Arctostaphylos* and *Ceanothus* (McMinn 1945) similar patterns can be found.

Based on these examples, the following hypothesis about evolutionary rates can be formulated following general principles set forth by Simpson (1944, chap. 4). In habitats which remain constant for long periods of time most of the plant groups tend to evolve more and more slowly, and some become altogether stagnant. These may belong to either primitive or highly evolved families, and may be either long-lived trees or annual herbs. There is no reason to believe, however, that such stable lines have necessarily lost their ability to produce genetic variants. Whenever their populations have been studied, considerable genetic variability has been found. And as was pointed out to the writer by Dr. J. T. Buchholz, artificial selection in one of the most famous of ancient relic species, the California big tree (*Sequoiadendron giganteum*), has yielded in a very few generations a host of variant types which are grown as horticultural curiosities. The stability of these lines is due to the fact that they are so well and broadly adapted to their environment that all new genetic types are less adaptive and are therefore eliminated by selection.

#### BASIS OF RAPID EVOLUTION

Rapid evolution requires the presence of a rapidly changing secular environment. But not all plant

groups exposed to such changes can respond to them by evolving. There must be present in the group not only genetic variability, but in addition gene combinations which are preadapted in the direction of the secular change. Thus in coastal California in recent geological time, rapid evolution has been chiefly in annuals, bulbous perennials, sclerophyllous shrubs, and other plants adapted to drought and highly seasonal precipitation. Suitable ecological niches for mesophytic perennial herbs are not lacking, and some of them, like *Aquilegia*, *Clematis*, *Dentaria*, *Saxifraga*, and *Cynoglossum*, are widespread and common. But they have not produced many species. The groups with preadapted gene combinations, in order to undergo rapid evolution, must also be able to evolve reproductive isolating mechanisms. Some xerophytic groups of coastal California, like the genera *Yucca*, *Heteromeles*, *Adenostoma*, and *Erysimum*, have undoubtedly become more abundant in individuals in recent times, but nevertheless have not produced many species. For one reason or another, they have lacked this ability to produce isolating mechanisms, and consequently, to evolve separate evolutionary lines.

#### THE FOUR MAJOR PERIODS OF ANGIOSPERMOUS EVOLUTION

##### DEVELOPMENT DURING THE CRETACEOUS

On the basis of the hypothesis of the control of evolutionary rates through interaction between the environment and the species population, we can explain to some extent the course of evolutionary change in the Angiosperm floras of North America. We should expect to find periods of rapid evolution alternating with times of relative stability, and this rapid evolution should be confined to particular types of plants. And this is precisely what has occurred. The first of these bursts of Angiosperm evolution came in the Cretaceous period, when the class first appears in the fossil record. At this time large numbers of species of Angiosperms, most of them belonging to modern families or even genera, largely displaced the preexisting Gymnosperms in nearly every known fossil locality. There is every reason to believe that the Angiosperms are considerably older than this first widespread appearance of them in the fossil record, but they must have been present in relatively small numbers and restricted to certain particular habitats. The extensive diversification of orders and families must have taken place during their period of increase. At this time, forests of a subtropical and tropical character were being stocked with angiosperms, so that woody plants adapted to these associations had a high selective value, and were on the ascendant. Furthermore, insects, particularly of the order Hymenoptera, were evolving rapidly at this time, so that various floral structures adapting plants to cross pollination by these insects also had a high selective value. In the Cretaceous period, therefore, all conditions favored the evolution of a relatively homogeneous type of plant as regards its vegetative structures, namely woody plants adapted



to subtropical or tropical forest conditions, but at the same time promoted great diversity in flowers and fruits. This explains the nearly simultaneous appearance of all of the major families of Angiosperms, and the fact that in most of them the primitive members are woody plants adapted to mild climates. With the exception of a temporary reversal during the Eocene epoch, the climatic trend since the Cretaceous period has been progressively less and less favorable to these primitive woody types, and as expected they have suffered much extinction and relatively little progressive evolution.

#### SITUATION IN THE MIDDLE AND LATER TERTIARY

The second burst of Angiosperm evolution occurred throughout the world in the middle and latter part of the Tertiary period, coincident with the raising of the great mountain systems of modern times, and the resulting increase of alpine and xeric habitats. This was accompanied by a general cooling of the earth's surface (Chaney 1940, 1947) and a consequent increase in the habitats available to plants adapted to temperate conditions. At this time, therefore, selection favored new kinds of vegetative structures, particularly shrubby and herbaceous types, as well as reduction of leaf surface and the deciduous habit. But new types of floral organization had relatively little selective value, except those adapted to pollination by wind and to seed dispersal by either wind or animals. Hence evolution would be expected to take place within the framework of the existing types of floral organization, with the principle innovations in the structure of the fruit and seed, but would produce many new and more reduced types of plants as to habit. This agrees with the evidence of a great increase in the number of species of shrubs and herbs, both annual and perennial, during the middle and latter part of the Tertiary period, and the accompanying diversification of fruit and seed types in certain families, such as the Cruciferae, Leguminosae, Umbelliferae, Boraginaceae, Compositae, Gramineae, and Cyperaceae. The contemporary rapid evolution of certain groups in coastal California is a late persistence of this mid-Tertiary evolutionary burst, aided by the climatic oscillations of the Pleistocene.

#### THE PLEISTOCENE AND ITS EFFECTS

The third of these evolutionary bursts accompanied the advance and retreat of the successive Pleistocene glaciations, with the accompanying extinction of plant species populations during the advance of the ice and the subsequent migration of the surviving types into the areas left open by the retreat of the glaciers. The evolutionary changes during this epoch were less than those of the previous periods of rapid evolution for two reasons. In the first place, the new climates which appeared were little different from those which had prevailed in northern and alpine areas before the glacial period, and in the second, the new habitats opened to colonization were mostly poor in nutrients, and little different from the habitats already existing south of the ice margin.

The new types favored, therefore, would be those having vigor, aggressiveness, an ability to grow well under poor conditions, and favorable combinations of the adaptive characters possessed by preexisting species. All of these conditions are realized by hybrids, and particularly by polyploids, so that evolution during the Pleistocene might be expected to involve chiefly allopolyploidy, and it is a recognized fact that the glaciated regions contain a particularly high proportion of polyploids. This was once thought to be due to the greater cold resistance of polyploids, but recent evidence indicates that this is not the case (Bowden 1940; Clausen, Keck, and Hiesey 1945). The great predominance of polyploids in the glaciated areas is therefore believed to be chiefly the result of hybridization and chromosome doubling involving species populations which came together after long periods of isolation in glacial refugia, and the selection of favorable gene combinations among the newly established polyploids. If this is true, then the majority of the polyploids in the glaciated areas should be found, when fully analyzed, to have an origin similar to that of *Iris versicolor* and *Oxycoccus quadripetalus*.

#### THE RECENT SITUATION

The fourth burst of plant evolution is just beginning. In the past few thousand years man has destroyed or altered the natural plant cover over millions of square miles of the earth's surface, opening up new, largely temporary habitats. Most of these areas have been occupied by species already preadapted to such habitats, which therefore become weedy with little or no evolutionary change. But some good examples are available of evolution now taking place as adaptations to the weedy condition. Most of these are on a relatively small scale, such as the acquisition of new genes by a species population through hybridization and introgression from another species, as in *Tradescantia* (Anderson and Hubricht 1938, Riley 1939), and the development of new hybrid, polyploid and apomictic types, as in *Vaccinium*, *Rubus* and *Crataegus*. But the stage is set for much more extensive evolution, so that the biologist looking for examples of evolutionary divergence just beginning or in rapid progress would do well to concentrate his attention on the plants which are colonizing the habitats being created by man.

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DISTRIBUTION PATTERNS IN MODERN PLANTS AND THE  
PROBLEMS OF ANCIENT DISPERSALS

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IN A SYMPOSIUM ON  
ORIGIN AND DEVELOPMENT OF NATURAL FLORISTIC AREAS  
WITH SPECIAL REFERENCE TO NORTH AMERICA

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# DISTRIBUTION PATTERNS IN MODERN PLANTS AND THE PROBLEMS OF ANCIENT DISPERSALS

## INTRODUCTION

The problems confronting those who seek to determine the origins and migration patterns of the organisms now present in any given region are many and varied. Because of the title of this symposium it has seemed wise to concentrate our attention in this discussion on what is now the dominant type of vegetation in North America—the angiosperms or flowering plants.

In developing this topic I have chosen to go somewhat beyond my original title and discuss—but briefly—certain items of a phyletic and historical nature. It is my belief that an areal distribution map, while interesting and often very enlightening, sometimes lacks significance unless some indication is given of the general trends in the relative specialization of the members of the group discussed.

Lacking adequate space, I cannot fully consider the criteria for determining relative specialization. However, I feel that the majority of us would agree that one of the general trends of phyletic divergence in flowering plants has been the loss or fusion of parts—that is, a trend toward condensation of the reproductive mechanisms. Another is the often noted transition from dehiscent, capsular fruits to indehiscent, baccate fruits; in many lines the highly specialized dioecious condition also is achieved. Any lengthy discussion of what constitutes “primitiveness” in the angiosperms or a listing of the usually accepted criteria, before this audience, would seem to be as unnecessary as arguing the question whether egg-laying was a “primitive” or “advanced” habit among vertebrates, or whether the single, functional toe of the living members of the horse line is a “primitive” or “specialized” condition. Therefore, it is hoped I will be pardoned if, in each instance presented, detailed reasons for assigning a relative position in the evolutionary scale to the various members of any particular group are not fully developed. To stay within the space allotted it has been necessary to sacrifice adequate consideration of these reasonably well understood criteria in order that a larger proportion of the many available examples might be presented. In various instances a partial list of the criteria is appended to the figures; these may serve to elucidate a few additional points.

## SOURCES OF DATA

Since the present paper is by no means intended as a summary of the whole field of angiospermous distribution the lack of anything like a complete bibliography will be immediately obvious. By omit-

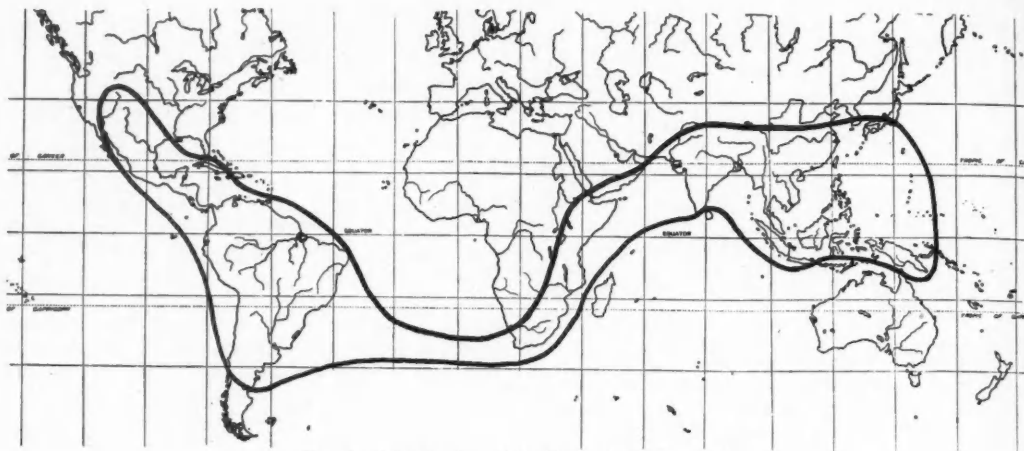
ting mention of a host of really important basic papers and works there is no intention to imply that they are not of great merit. The apparent lack of what might be termed the “scholarly approach” to this problem has been a conscious one; it has stemmed from a desire on my part to reexamine the basic data with, perhaps, a minimum of influence from the conclusions of others. In compiling the data presented in this paper considerable use has been made of the facilities of the Herbarium of my own institution; in addition, I have borrowed freely from such standard and well-known works as Engler and Prantl, *Die Pflanzenfamilien*; Engler, *Das Pflanzenreich*; Hutchinson, *The Families of Flowering Plants*. I. Dicotyledons (1926), II. Monocotyledons (1934); and the series of 303 maps recently presented by Vester [*Die Areale und Arealtypen der Angiospermen-Familien*, Bot. Archiv. 41. 1940]. The cytological data were taken from the recent book by Darlington and Janaki-Ammal:—*Chromosome Atlas of Cultivated Plants*, London, 1945. The maps of the various monocotyledonous groups—here necessarily generalized—have been constructed more from data gleaned from an examination of Hutchinson's work than from any other source. I also wish to acknowledge the inspiration gained from long conversations on this subject with my former associate, C. L. Gilly. Although various systematists may not agree with the groups as here outlined, it has seemed impractical for the present to attempt any coordination between the latest studies (often regional and therefore incomplete) with any group as a whole; for the purposes of our present study the general phyletic trends within a group would seem to be quite as important as an analysis of the more recent generic and specific delimitations.

The stippled map used was published by Ginn and Company, Copyright 1924; the other was from the McKinley Publishing Co., Philadelphia. In both maps it was sometimes necessary to cut and rejoin the parts to obtain the projection needed.

## A REVIEW OF THE DATA

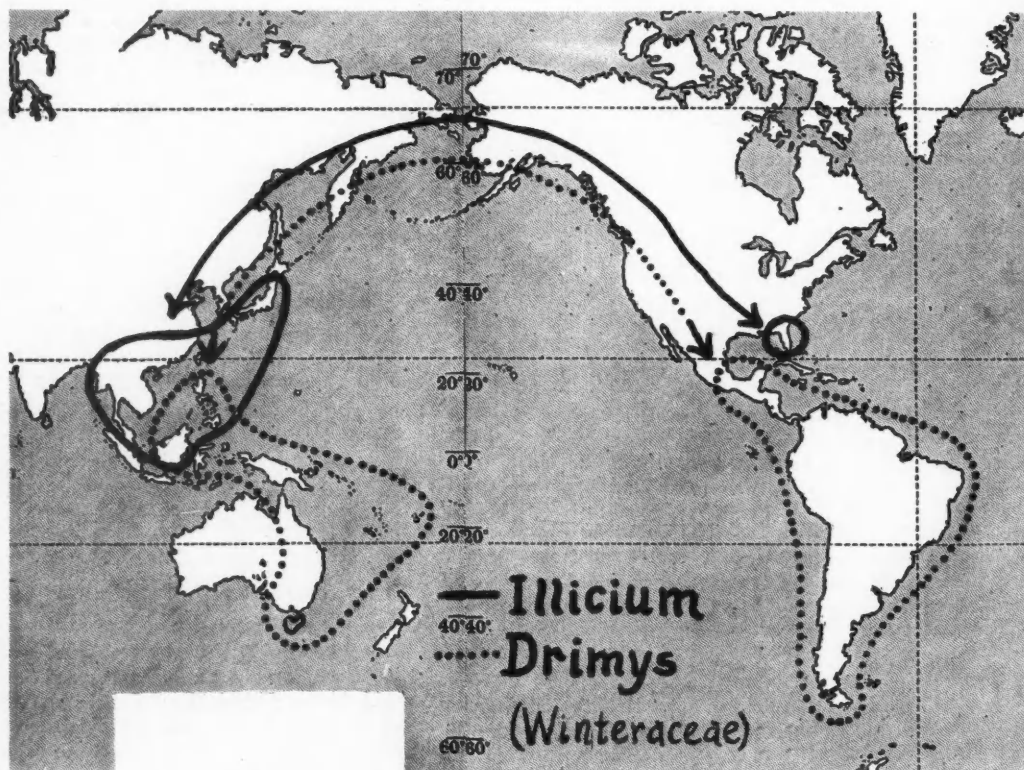
### THE PROBLEM CONFRONTING US

Let us, then, turn directly to a consideration of some of the types of distribution which are commonly found in the angiosperms. For our first example we will take *Buddleia* (Fig. 1). Here is a genus, wide spread in the tropics, with groups of derived species which tend to enter both drier habitats and temperate regions.

FIG. 1. Distribution of *Buddleia* (Loganiaceae).

In *Illicium* and *Drimys* (Fig. 2) we have two genera which belong to a group usually thought to be members of the old Magnolialean complex. With the presence of numerous magnolioid fossil remains in the North, even in what is now the subarctic, it

would be only logical to assume that the region of the old Bering Land Bridge at one time was climatically favorable for the development of organisms which now are able to exist only considerably farther south.

FIG. 2. Present disjunct distributions and possible migration routes of *Illicium* and *Drimys*.



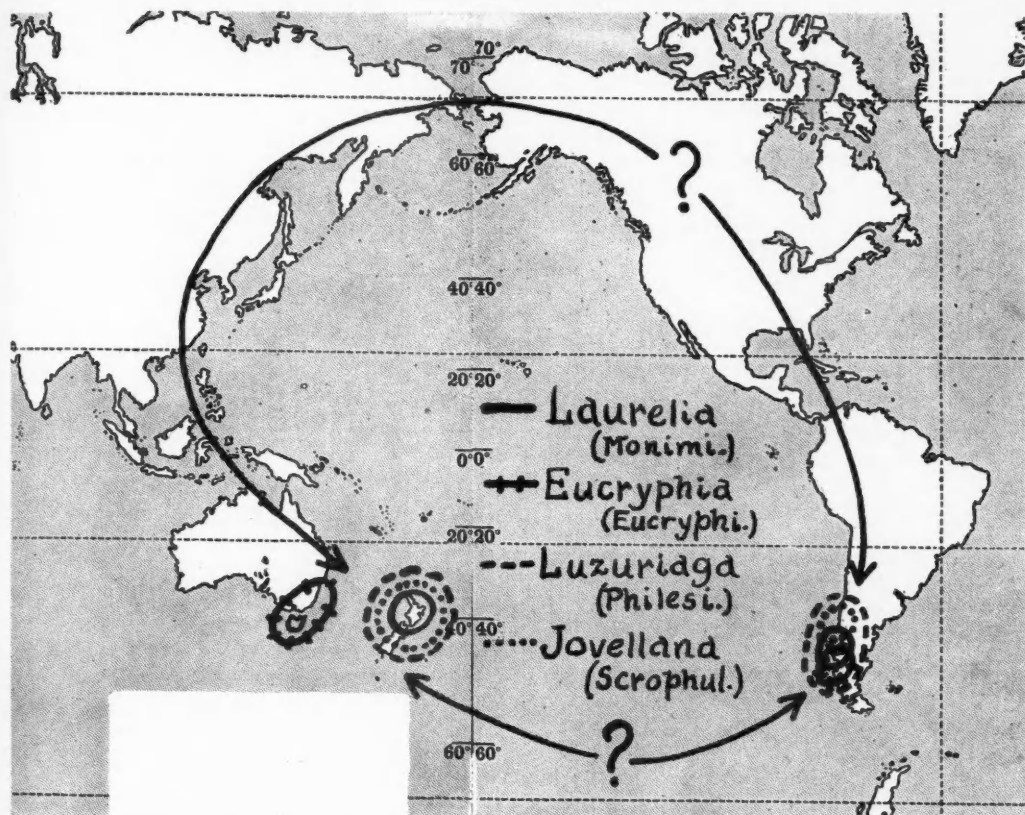


FIG. 3. Present disjunct distributions of Laurelia, Eucryphia, Luzuriaga, and Jovellana.

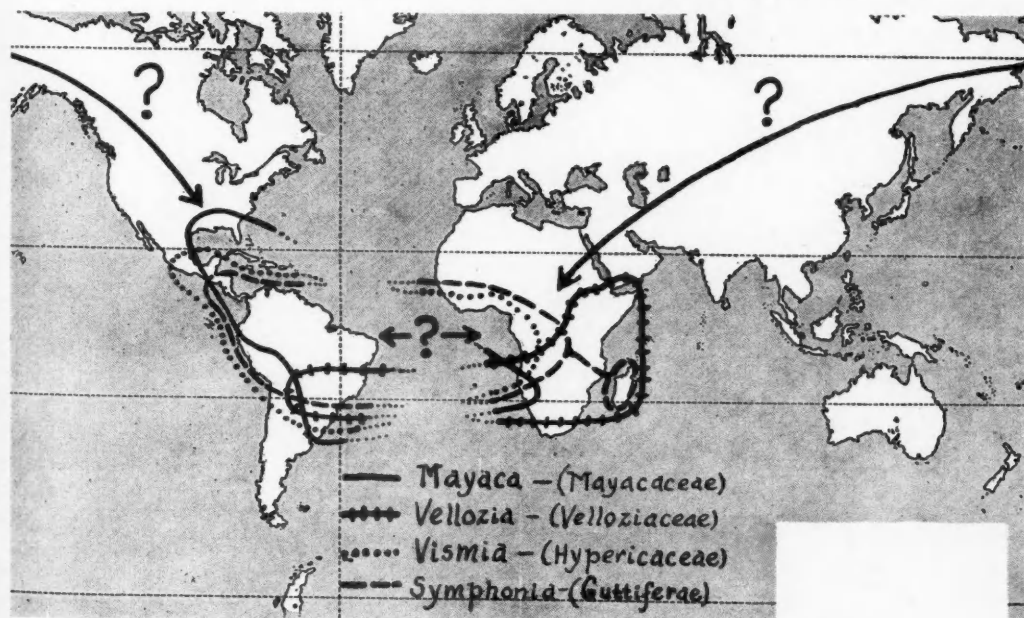


FIG. 4. Present disjunct distributions of Mayaca, Vellozia, Vismia, and Symphonia.

This Bering Land Bridge, an ancient intercontinental connection, seems to be so well established and authenticated by a variety of evidences that I need spend no more time discussing it. However, I would call your attention to the southernmost limits of the genus *Drimys*, in Tasmania and southern South America. With these in mind, let us look at only a few of the numerous examples which might be used of another fairly common distribution pattern (Fig. 3—see also Footnote No. 1). Are genera such as these, with their bi-areal distributions far to the south, the remnants of a once much wider distribution in northern regions? Or, at some time in the past, has there been a land connection directly between Australia, New Zealand and South America?

Another frequent distribution which confronts us with problems is the Afro-South American pattern (Fig. 4). These examples are not unique; there are many more quite like them.<sup>1</sup> Have genera such as

<sup>1</sup> Twenty years ago, Good—A summary of discontinuous generic distribution in the Angiosperms. *New Phytol.* 26: 249-259, 1927—pointed out that no less than 64 genera have this general distribution. Had he listed the closely paired genera—which, if their species all were on one side or the other of the Atlantic long ago would have been generically combined (but are left apart primarily through inertia or tradition)—his list would have been considerably enlarged. The same is true of another connection, that between South America on one hand and New Zealand, Australia and/or Australasia on the other, where he lists only 28 genera.

these achieved their present ranges by migration across the Bering Land Bridge, accompanied by a subsequent loss of connecting forms? Or has there been a direct connection at some time in the past directly between Africa and South America?

#### A POSSIBLE EXPLANATION

Before we proceed with this discussion, let us first look at what, if I am able to judge, is the generalized concept, held by many, of the history of the development and dispersals of various angiospermous stocks (Fig. 5). With relatively abundant series of fossil remains in northern regions there would seem to be evidence that the primitive types arose in what is now the north, spread and occupied all the available area, venturing into the southern regions wherever land areas became available. Subsequently, from these primitive forms the more advanced groups arose and, presumably because of the advantage of their specialization, were able to supersede the more primitive forms in much, but perhaps not all, of their ranges.

Later, probably because of the vicissitudes of climatic deterioration, even the more advanced groups sometimes became limited in distribution. Today (as in Fig. 5D), we find fossil examples of the relatively primitive members of such groups in the north, to-

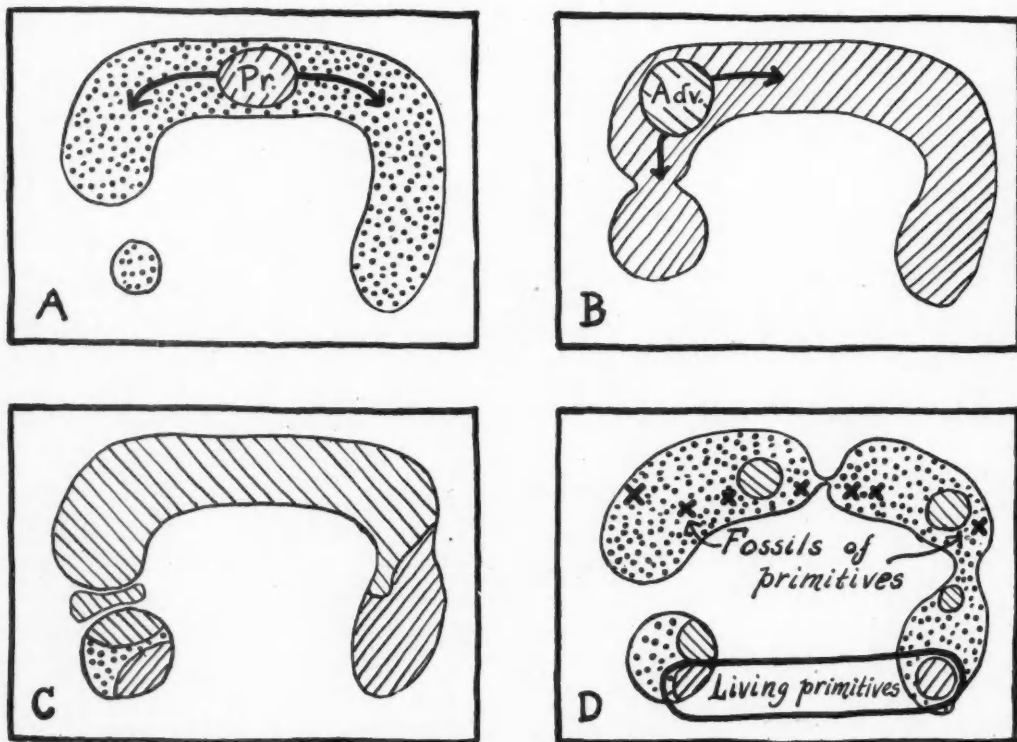


FIG. 5. Possible history of the dispersal of an angiospermous group. Dots—areas unoccupied by the group at various times. Pr.—primitive forms. Adv.—advanced forms. Crosses—fossil forms of primitive types.

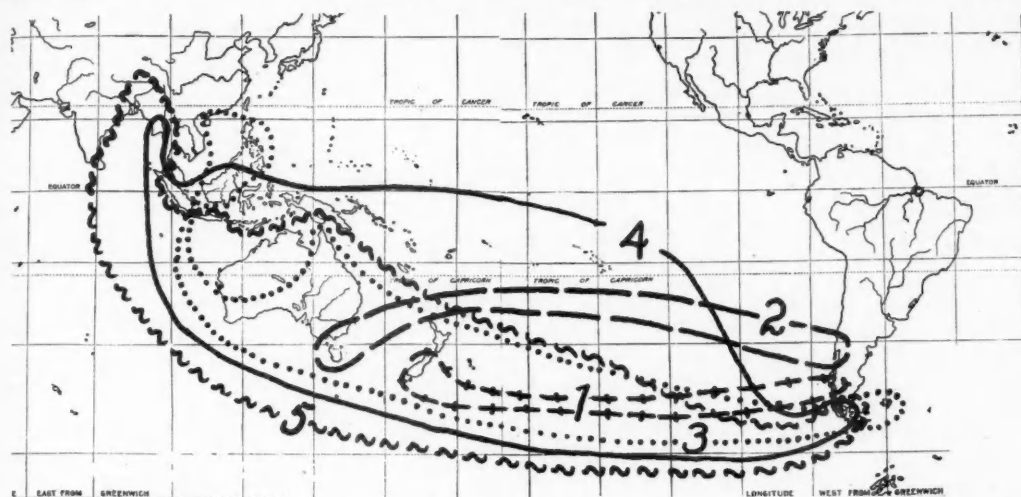


FIG. 6. Distributions of 5 families. 1—Tetrachondraceae; 2—Eucryphiaceae; 3—Centrolepidiaceae; 4—Epacridaceae; 5—Stylidiaceae.

gether with the now disjunct living examples of the more advanced members. In the southern regions, in many instances, there also are to be found living examples of both relatively advanced and primitive types. Naturally, the possible permutations of the sequence in the first three figures of this series are numerous; but the picture presented by so many groups is so similar to that in Figure 5D that we might easily come to the conclusion that some variation of the earlier sequences must have taken place. However, the possibility that we might be in error should not be overlooked. With this for an introduction to our problem, let us now hastily examine various groups in some detail for such evidence as they may yield.

It should be kept clearly in mind that it is not implied here that the modern species with relatively primitive characters gave rise to the modern advanced species; these maps merely indicate general tendencies.

#### THE PATTERNS CENTERING AROUND THE AUSTRALIAN REGION

Here, in Figure 6, are five families of angiosperms which have a southern distribution. To these could be added quite a large series of genera in otherwise much more widely dispersed families; closely paired species and even common species also are said to occur. Did all these achieve their South American localities by migration across the Bering Land Bridge? Or was there once a southern land-connection?

Here in the Restionaceae (Fig. 7) each circle indicates a genus, most of them left unnamed. Some are local, others more widespread. What was the track which *Restio* took in moving from Australia to South Africa? (Or *vice versa*?) What was the route taken by the American representatives of *Leptocarpus*? To avoid monotonous repetition, I trust that we will ask ourselves much the same question each time we meet such disjunctions.

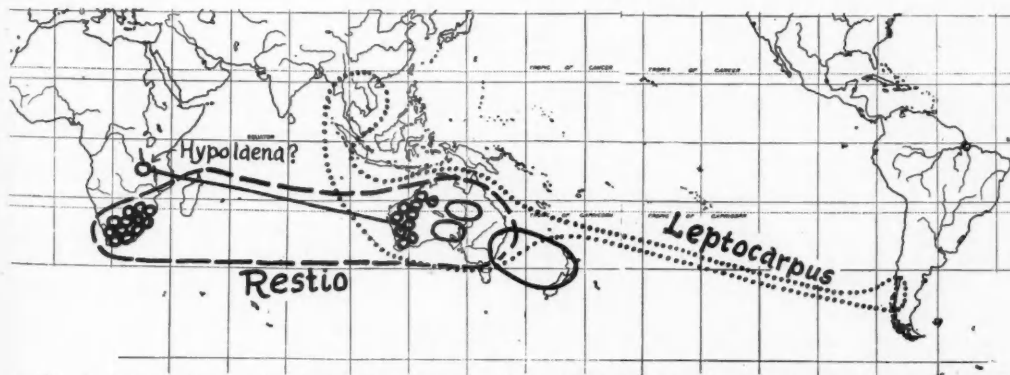


FIG. 7. Distribution of the family Restionaceae. Each circle indicates a genus. The S. African genus *Phyllocladus* and the Australian *Leprodia* are said to have species with primitively hermaphrodite flowers, an unusual condition in this family.

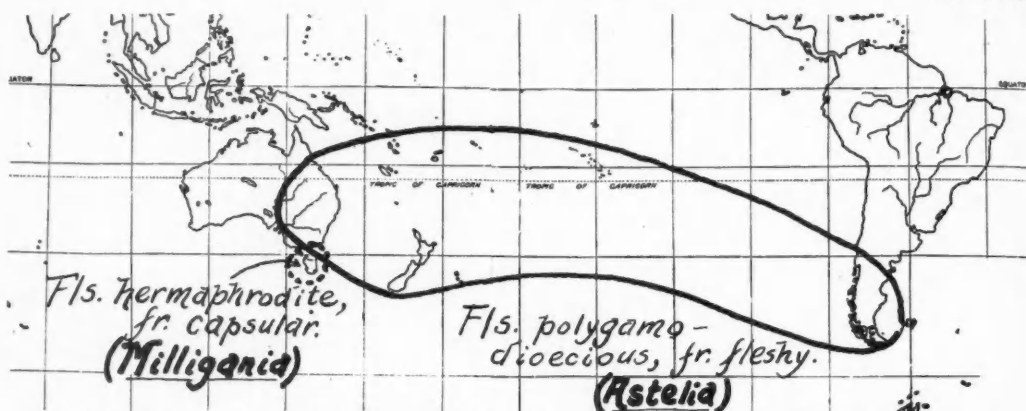
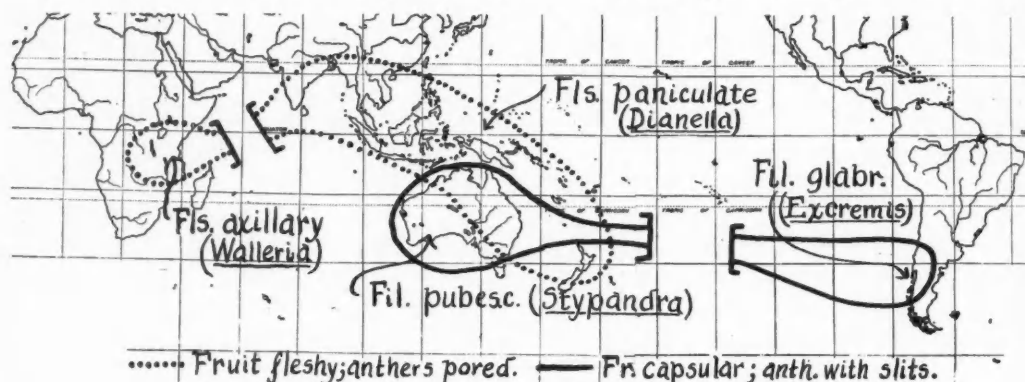
FIG. 8. Distribution of the Tribe Milliganieae of the Liliaceae. The more primitive *Milligania* is Tasmanian.

FIG. 9. Distribution of the genera of the tribe Dianelleae of the Liliaceae.

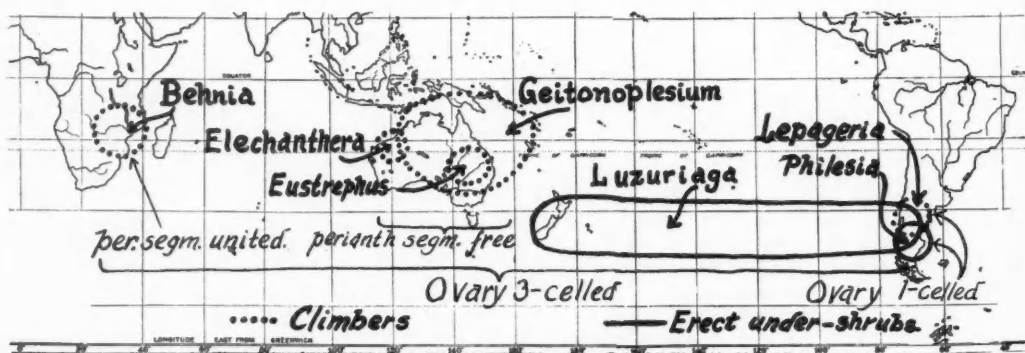


FIG. 10. Distribution of the genera of Philesiaceae.

The tribe Milliganieae of the Liliaceae is small, containing but two genera (Fig. 8). Here the Tasmanian genus, *Milligania*, is patently primitive; *Astelia* is the derived genus.

Another tribe of the Liliaceae, the Dianelleae, is also southern (Fig. 9). The distribution, in Australia and Chile, of the paired, more primitive genera of this tribe is marked by the solid line; the paired, de-

rived genera (marked by the dotted line) extend from New Zealand to Africa.

In the Philesiaceae (Fig. 10), the genus *Luzuriaga*, on several counts, deserves to be classed as the most primitive. From it, in South America, have been derived two local and specialized genera. Another tract of divergence from *Luzuriaga* trends westward, by way of the Australian lianoid genera, to its culmination in the African genus *Behnia*.



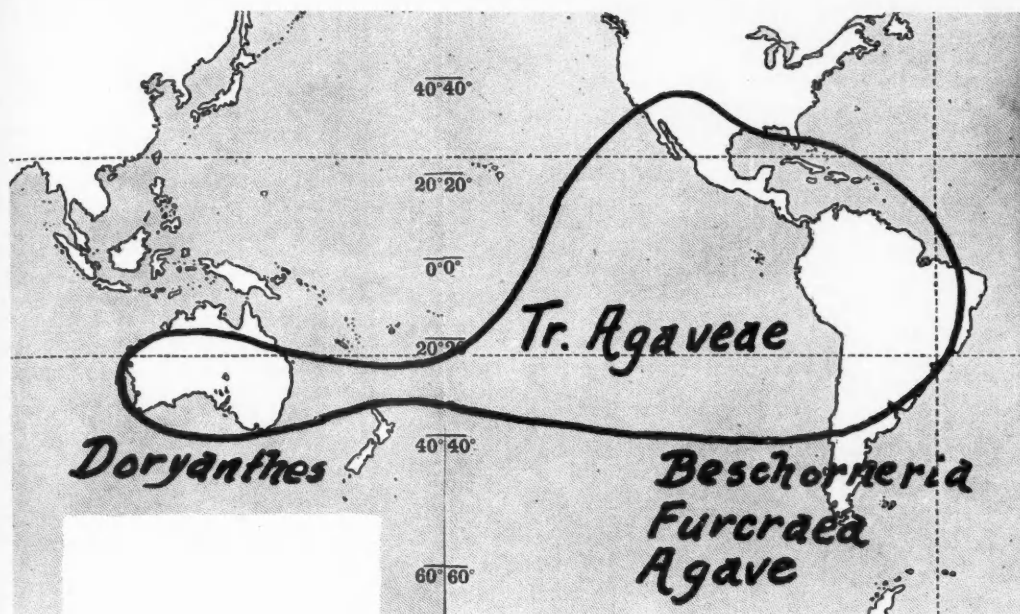


FIG. 11. Distribution of the tribe Agaveae.

Coming closer home and to plants perhaps somewhat more familiar, we have the tribe Agaveae, to which our Century-plants belong (Fig. 11). There are three genera in the Western Hemisphere; the fourth genus—and perhaps the most primitive—is the Australian *Doryanthes*.

Many students of plant distribution hesitate to deal with aquatic groups, perhaps on the assumption that they would be doing little else than mapping the mi-

gration routes of aquatic avi-fauna, which have long been suspected as the major dispersal vectors. While many aquatics do have wide dispersals, I feel that a study of these groups will yet yield very pertinent information.

One example is the Halorrhagaceae (Fig. 12A) represented in eastern North America by the ubiquitous *Myriophyllum* and also by the distributionally more limited *Proserpinaca*. When we examine this

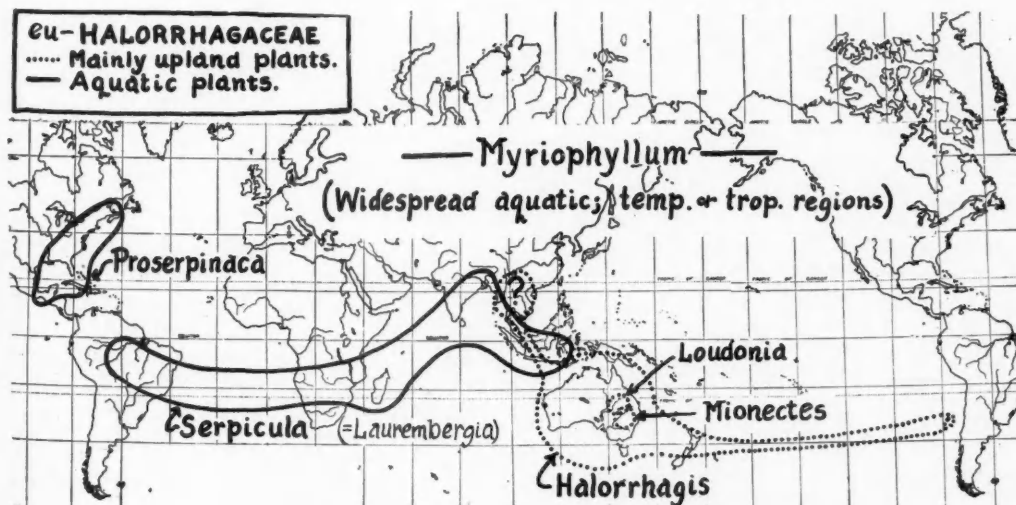


FIG. 12A. Distribution of the genera of the eu-Halorrhagaceae.



part of the family carefully we find that, on the basis of its morphological structure, *Halorrhagis* appears to be the most primitive living member. In Australia two derivative genera are to be found. While present in southeastern Asia, I have been unable to ascertain the exact distribution of *Halorrhagis* in that region. Although *Halorrhagis* seems not to be primarily an aquatic, some of its species do have distinct paludous tendencies. On the basis of its morphology, the aquatic *Serpicula* appears to tie-in rather directly with the sub-aquatic members of *Halorrhagis*; trending westward, the tropical *Serpicula* appears, metaphorically, to be pointing its finger directly at the derived, mainly temperate, eastern North American *Proserpinaca*. (This Africa—South America—eastern North America phyleto-dispersal pattern is not at all unusual in angiosperms.) *Myriophyllum* appears to be a further aquatic derivative from the basic halorrhagoid line.

[NOTE: In preparing Fig. 12A from miscellaneous notes several errors were copied. Apparently *Serpicula* also is found in north Africa. *Loudonia* seems to be primarily (if not entirely) in west Australia; also *Meionectes* (the "Mionectes" of the chart) is found in both southern Australia and Tasmania.]

Keeping *Halorrhagis* in mind (its distribution repeated here for clarity), we will examine the other members of this phylad (Fig. 12B). Here I can do no more than call your attention to the relation between the distribution pattern of *Gunnera* to that of *Halorrhagis*. *Hippurus*, which we sometimes think of only as a north temperate and subarctic group, occurs as far north as Greenland; however, it is also recorded from Australia and recently I have come

across unconfirmed rumors of collections of the genus in Antarctic South America.

Another aquatic group is the *Juncaginaceae* (Fig. 13). The most primitive living member of this family is the Australian *Cynenogeton*, from which *Triglochin* appears to be a close derivative. I would call your attention, especially, to the Antarctic distribution of *Triglochin*, and its present connection with the northern segment of its population. Also, I would call your attention to the location, in Patagonia, of the dimerous and dioecious flowered *Tetroncium*, and the genus *Maundia* in Australia, with (in this family) its uniquely reversed ovules. Here, then, in *Tetroncium* and *Maundia* are two highly divergent "experiments" in basic evolution which have been carried on by this family of plants. Let us remember the geographical relation of these to the primitive *Cynenogeton*. More will be said at another place in this discussion concerning the geographical relationships between the primitive members of our angiosperms and these (what we might call the) advanced, evolutionary "trial balloons."

With the distribution of the Australian *Cynenogeton* in mind, we will turn to a closely related and probably derived aquatic family, the *Zannichelliaceae* (Fig. 14). Here there are two groups of genera, one, the more primitive (shown by the dots), occurs in fresh and brackish waters; the derived group of genera, specialized on several counts, is entirely marine. Of the first group, the Australian *Lepilaena* appears to be the most primitive; apparently from it there has been a development to the essentially cosmopolitan *Zannichellia* from which, in turn, *Althenia* of the Mediterranean region seems to have been derived.

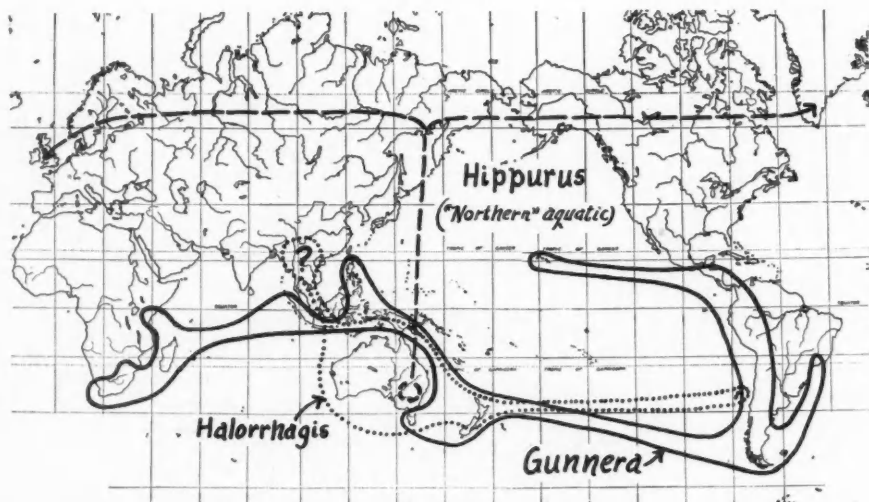


FIG. 12B. Distribution of the genera *Gunnera* and *Hippurus* relative to that of the more primitive *Halorrhagis*. These two genera are sometimes segregated as two separate families distinct from the *Halorrhagaceae*.

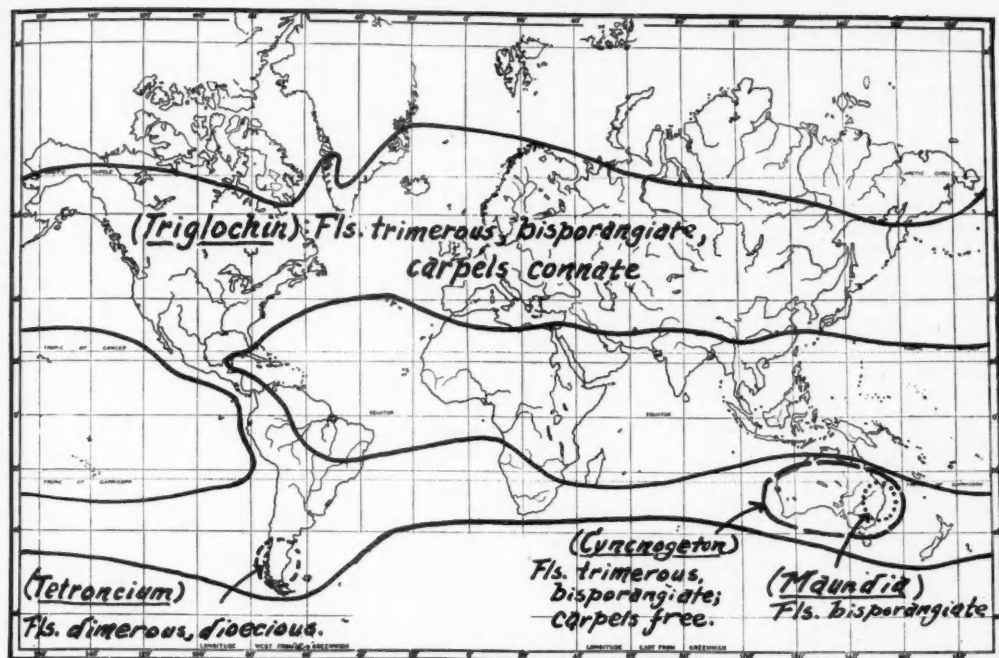


FIG. 13. Distribution of the genera of Juncaginaceae. Note: In all genera the ovules are erect except in the Australian *Maundia*, where they are pendulous.

The marine genera of the Zannichelliaceae apparently are most commonly met with in the Australian region; *Cymodocea* today is widespread, on the other hand *Amphibolis* ranges only from Australia westward into the Indian Ocean, whereas *Diplanthera* ranges both westward from Australia into the Indian

Ocean and eastward into Polynesia, appearing again in the Caribbean region.<sup>2</sup>

<sup>2</sup> Students of both fossil and modern marine animals may be interested in the parallel between the distribution of *Diplanthera* and some of their forms. It would appear that the Central American, Tertiary, marine "break-through" is here corroborated by the distribution of a living, marine, flowering plant.

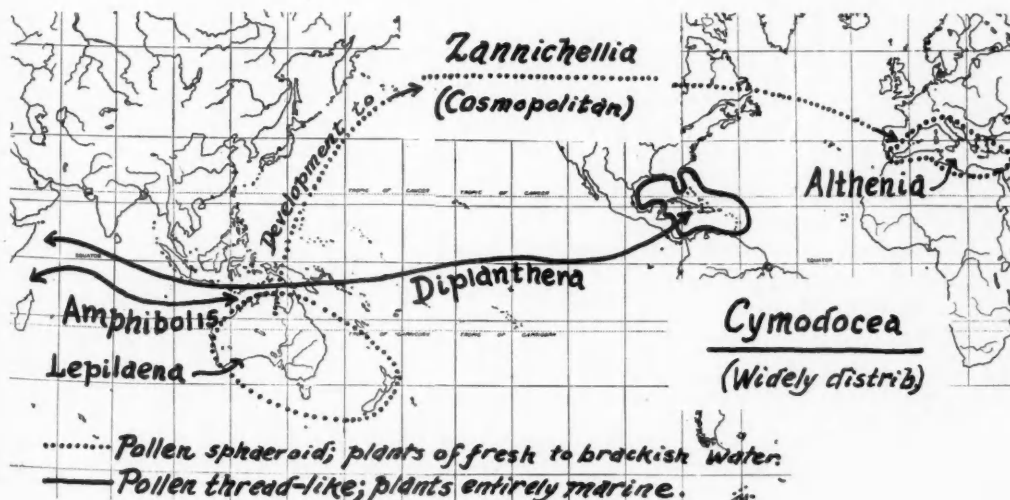


FIG. 14. Distribution of the genera of the Zannichelliaceae.

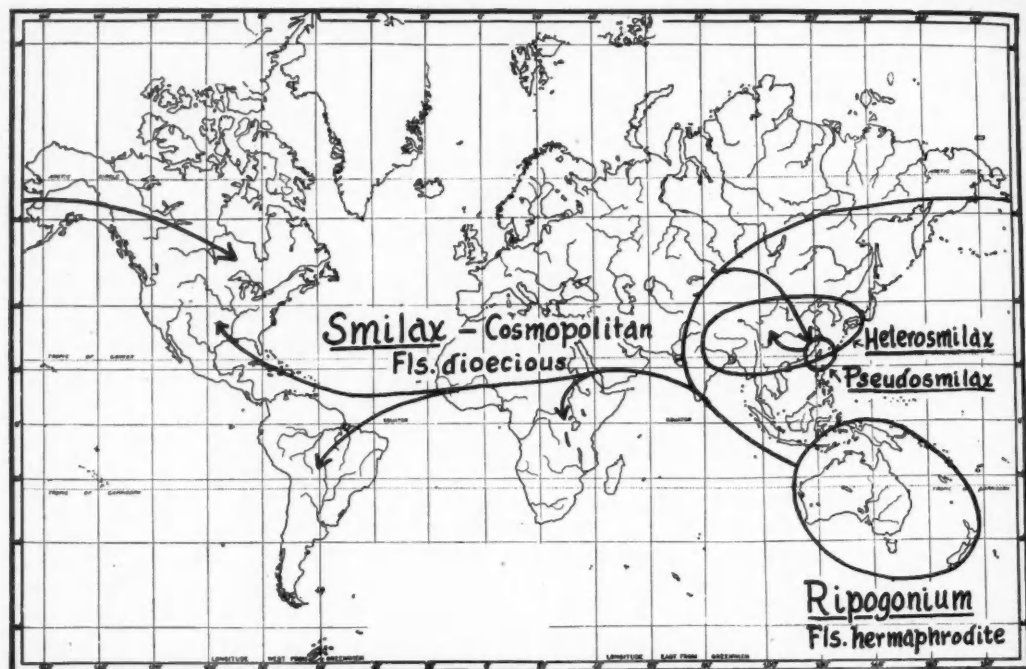


FIG. 15. Generalized distribution of the Smilacaceae. In *Ripogonium* the flowers are hermaphrodite; in all other genera they are dioecious. Other morphological characters indicate a development from the cosmopolitan *Smilax* to *Heterosmilax* and *Pseudosmilax*, and also to the North American members of the group with annual, aerial stems.

But, lest we become submerged in a study of aquatics which, as may be seen, can have quite logical distributions, let us close this part of our discussion with a consideration of one other group, the more familiar and almost ubiquitous "cat-briers" or smilaxes (Fig. 15). The genus *Smilax* is essentially cosmopolitan, having given rise, in Asia, to two somewhat localized derivatives.<sup>3</sup> These, with their immediate precursor, *Smilax*, are dioecious; the primitively hermaphroditic (bisporangiate) member of this family is the genus *Ripogonium* of Australia and neighboring areas.

So much, then, for a few of the examples of the distribution patterns of groups which, to a large extent, have their living primitive members in the Australian region.

#### THE MADAGASCAR-INDOMALAYAN PATTERN

The Madagascar region also seems to be a rich area for our investigations. For a long time the peculiar monocotyledonous genus *Trichopus* was hanging apparently in phyletic mid-air, with no close relatives. The comparatively recent discovery of the genus *Avetra* in Madagascar (Fig. 16) has now given us the means of relating *Trichopus* with more normal-appearing, southern-hemisphere, monocotyledonous types.

<sup>3</sup> The North American species with annual, aerial branches and two ovules also are sometimes nomenclaturally segregated from *Smilax*.

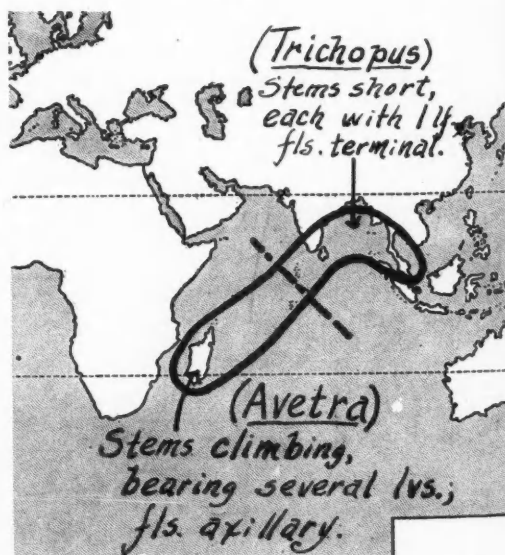


FIG. 16. Distribution of the Trichopodaceae.

This Madagascar-Indomalayan distribution pattern (often with outliers in Africa and Australia)

recurs frequently.<sup>4</sup> If it is not stressed in this discussion it is not because it is neither interesting nor important; the limitations of space demand that, for the most part, we pass it by. Also, it is perhaps not so immediately important in a consideration of the problems encountered in the present symposium.

#### THE AFRO-SOUTH AMERICAN PATTERN

The Velloziaceae brings us somewhat closer to our general topic (Fig. 17). Here, in this compact, small family, the primitive genus *Vellozia* is found in Africa and South America; the derived genus, *Barbacenia*, occurs only in South America.



FIG. 17. Distribution of the Velloziaceae.

The many genera of the widespread, tropical Marantaceae are divided into two almost equal tribes (Fig. 18). The more primitive of these is the predominately Afro-Asiatic Phryneae, one genus of which, *Calathea*, is in South America. The more specialized and morphologically reduced tribe, the Maranteae, has a single genus, *Thalia*, common to Africa and South America; the other genera of this derived and divergent tribe are all in South America.

<sup>4</sup> Examples of this pattern may be seen in the works of Hutchinson and Vester (*loc. cit.*); the eastern sectors of the area have been (and are being) treated by such well known students as Lam, Merrill, and Van Steenis.

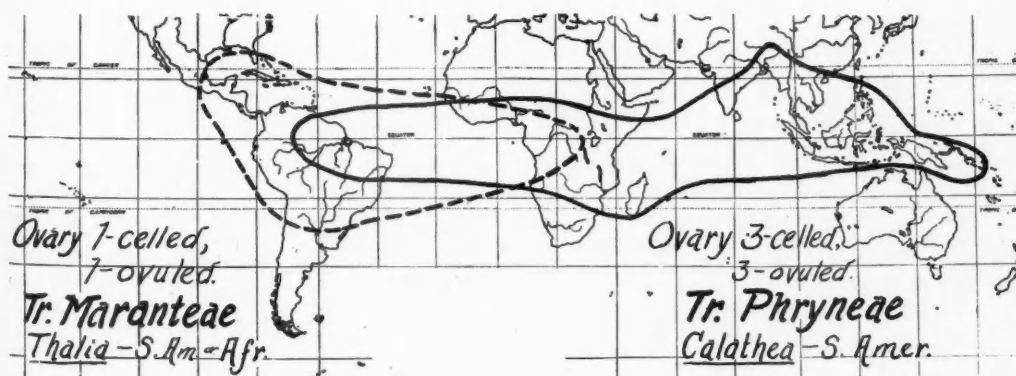


FIG. 18. Distribution of the Marantaceae.

Considering briefly another aquatic group, let us turn to the Pontederiaceae (Fig. 19). Its patently primitive genus, *Monochoria*, is found from Australia through tropical Asia into Africa. Here on the chart I have not so much plotted the distribution of the other genera as a series of general divergences from the basic monochorioid stock. The present figure is by no means satisfactory. A more recent re-evaluation of the basic data indicates the need of showing in more detail the two divergences from the primitive monochorioid stock, one of which reaches its culmination in the 1-stamened Brazilian *Hydrothrix*, the other in the zygomorphic-flowered *Pontederia* of eastern North America.

In the Strelitziaceae (Fig. 20), *Ravenala* is usually conceded to be the most primitive genus. Associated with it (and enclosed by the solid line) are the other members of the family with a common set of relatively primitive characters; the derived and highly divergent group is represented by the entirely American genus *Heliconia*. It is perhaps of some interest to note that the relatively primitive genus *Ravenala* has a basic chromosome number of 11; of the two species of *Strelitzia* studied, the larger, more ravenaloid one also has the basic number of 11, the more reduced and divergent species, *S. Reginae*, has 7. No count is known for *Phenakospermum*. In *Heliconia* the basic number of 11 is again found, with counts of 8 and 12 also appearing.

#### SOME OBSERVATIONS ON CYTO-GEOGRAPHY BASED ON INCOMPLETE DATA

Now I am not a cytologist and therefore have no justification, except out of curiosity, to be concerning myself with chromosomes. But in view of some of the distribution patterns which we have just seen, it is my opinion that, when data on more groups becomes available they will yield interesting results when mapped in correlation with the relative specialization of the genera, or even of the species within a single genus.

For example, in *Malvastrum*, one of the mallows,



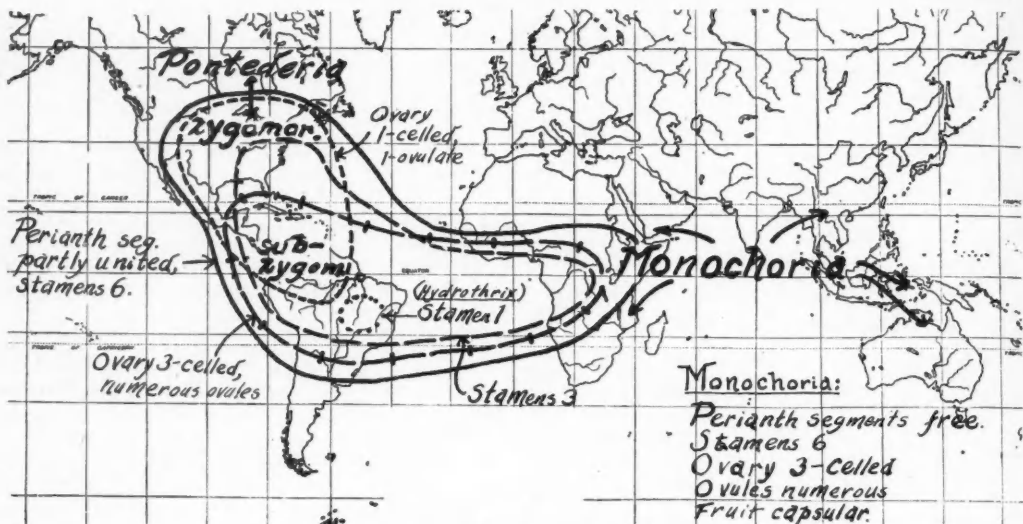


FIG. 19. Distribution of the Pontederiaceae.

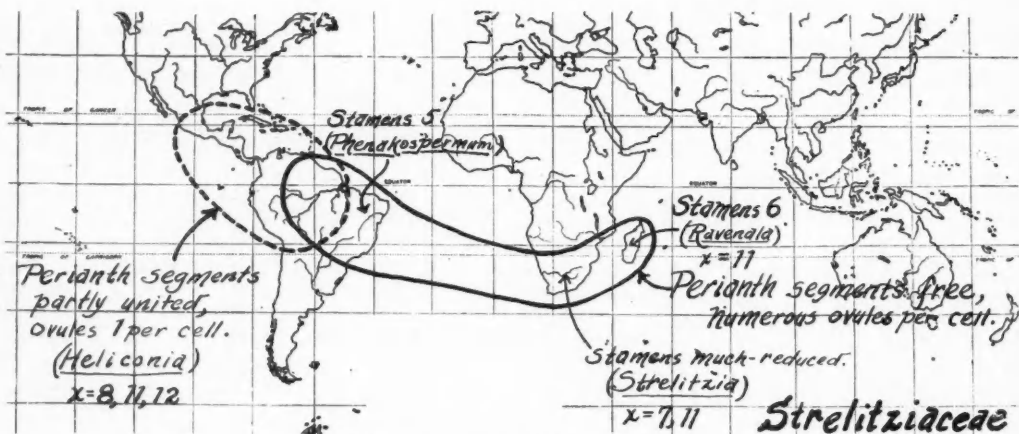


FIG. 20. Distribution of the Strelitziaceae.

a series of different numbers has been found. Knowing nothing about the intra-generic phylogeny of this group, I have merely put a line around the general geographical localities of those species with the same basic chromosome number (Fig. 21). Even so, a rather interesting pattern emerges. Looking at this chart you may note that the lowest known basic number, 11, occurs in South Africa; and that there is a general trend away from this area by way of the 12-, 15- and 17-chromosome groups, with a secondary high-number series of 21 in Africa.

The closely related genus *Hibiscus*, so far as the counts available to me indicate, has much the same pattern (Fig. 22). The lowest, 7, occurs in South Africa; the next, 11, in southeastern tropical Asia; a 15 group is common to Africa and southeastern Asia; groups of 17 and 18 are much more widespread

in the tropics; and a series of 19-chromosome species is found in North America and Spain. High-number (20-chromosome) groups are found in temperate eastern Asia, and (much as in *Malvastrum*) again in Africa.

In the genus *Impatiens* (to which our common garden Balsams belong) the general pattern is again much the same (Fig. 23). It is perhaps of some interest to note that the European 10-chromosome group, represented by *Impatiens Noli-tangere*, morphologically is a very close homolog of our two eastern North American species, both of which have the same basic number. When this chart was made I marked the European region as having material with "extra" chromosomes. I have since tracked these down with more exactness; the numbers respectively are 11 and 12, and their distributions are "Siberian."



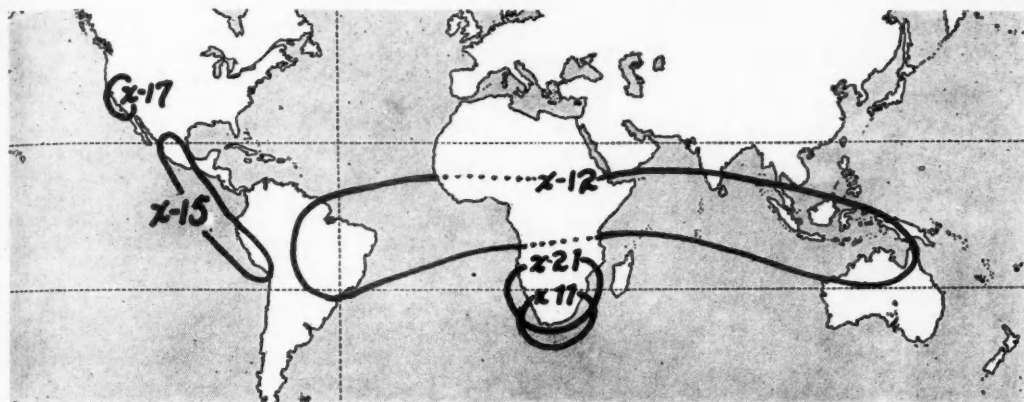


FIG. 21. Distribution of the known chromosome numbers in *Malvastrum*. The lines enclose those areas where species with the same basic chromosome number occur and do not necessarily indicate phyletic sequences.

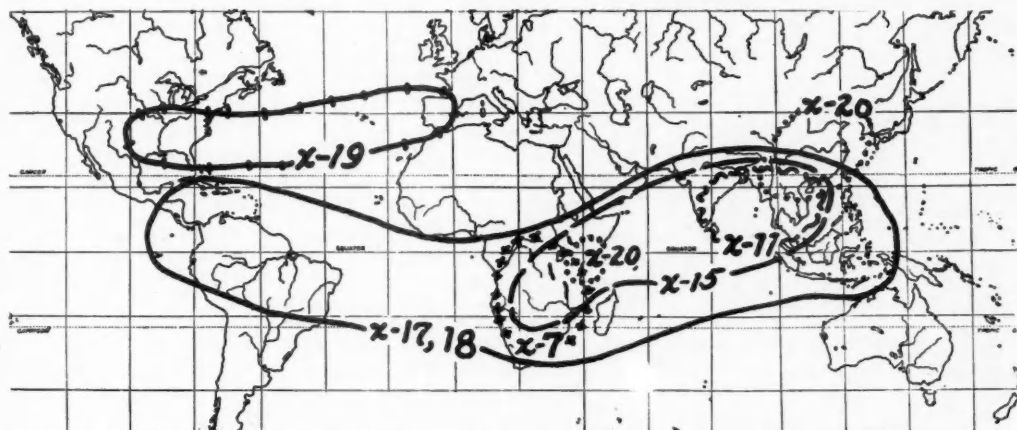


FIG. 22. Distribution of the known basic chromosome numbers in various species of *Hibiscus*.

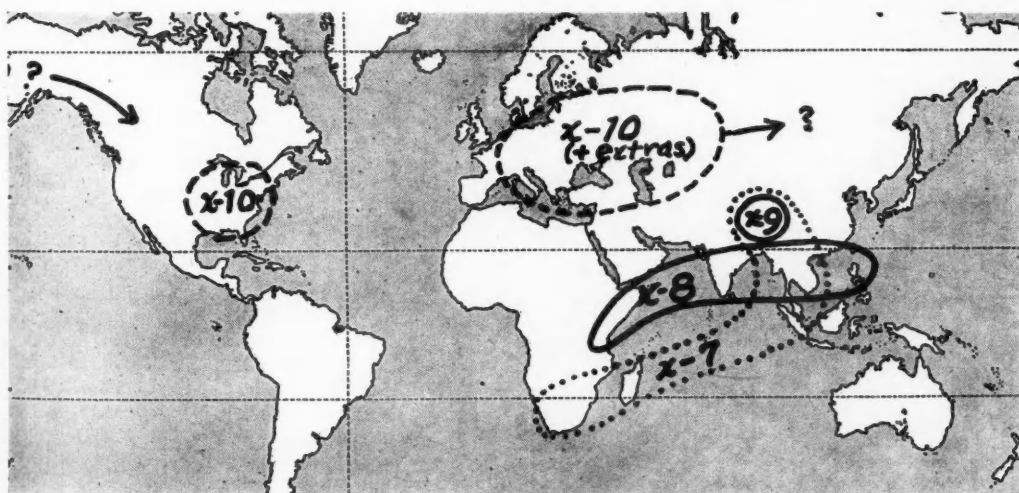


FIG. 23. Distribution of the known basic chromosome numbers in *Impatiens*.

I am certain that I do not know the significance of this general south-north trend in the increase of basic chromosome numbers in these genera. Possibly it is no more than coincidence resulting from a lack of complete data, but I suspect not.

#### EXAMPLES OF THE PATTERNS CENTERING IN SOUTH AMERICA

Leaving Africa for the time being, we now turn to another area which appears to have been a repository of primitive types, to tropical South America.

Here in the aquatic Butomaceae (Fig. 24) we have such things as *Hydrocleis*. Now I would not have you think that I believe *Hydrocleis* to be the immediate ancestor of the other Butomaceae, but I do feel that it is not too unlike what might have been the ancestral form of the group. Such things as *Tenagocharis* and *Butomus* certainly seem to have diverged from such a basic stock.<sup>5</sup> So far, all too little is known of the cytology of this group; however, a somatic count of 12 chromosomes is known for *Hydrocleis*, and counts of 26, 28, and 40 have been made in *Butomus*.

If, so far, I seem to have stressed monocotyledonous groups, or aquatic groups in both the monocots and dicots, it is not because they yield a peculiar type of information; I have presented data from them solely to demonstrate that these usually neglected groups do not fundamentally differ in their distribution patterns from the often woody dicotyledonous groups, on which so much study already has been done.

Let us, for example, take the Tea Family, Theaceae

<sup>5</sup> Under natural conditions, partially stranded plants of *Hydrocleis* often have condensed, bracteate flowering branches highly suggestive of the crowded inflorescence of *Butomus*.

(or Ternstroemiaceae; Fig. 25). It is almost impossible to open any text discussing general dispersals without finding *Stewartia* used as a stock example of a bi-areal distribution. However, the same situation is also present in the related genera *Gordonia*, *Haemocharis*, *Taonabo* and, to a large extent, also in *Eurya*. These, with a scattering of other genera in Asia (here incompletely indicated and then only in a generalized manner by means of arrows), together with the outlying *Adinandra* and *Vismea*, apparently constitute the more advanced members of the family. They seem to have been serially derived from the South American *Bonnetieae*, represented today by *Archytaea* and *Bonnetia*. The somewhat primitive Madagascan *Asteropeia* seems to have had little, if anything, to do with the development of the more advanced members of the family.

If space permitted, I should (as may well be suspected) like nothing better than to discuss at great length my favorite family of plants, the Ericaceae. Remembering the distribution of the primitive Bonnetieae, let us look at some of the Ericaceae (Fig. 26), a family usually thought to have been rather directly derived out of the same basic stock as the Theaceae. So far as I can judge, the genus *Befaria* (indicated by dots) is the most primitive living member; it is so close to the Tea family that, in a recent study of the genus, it was necessary to extract some of the material from the Theaceae where it had been (and perhaps not too erroneously) recently described as a new genus.

It is of considerable interest to note that, in *Gaultheria* and *Pernettya*, there seems to be a concentration of diploid species in the far south; in one section of *Gaultheria*, the most northerly species (*G. shallon* of our North American west-coast) is an

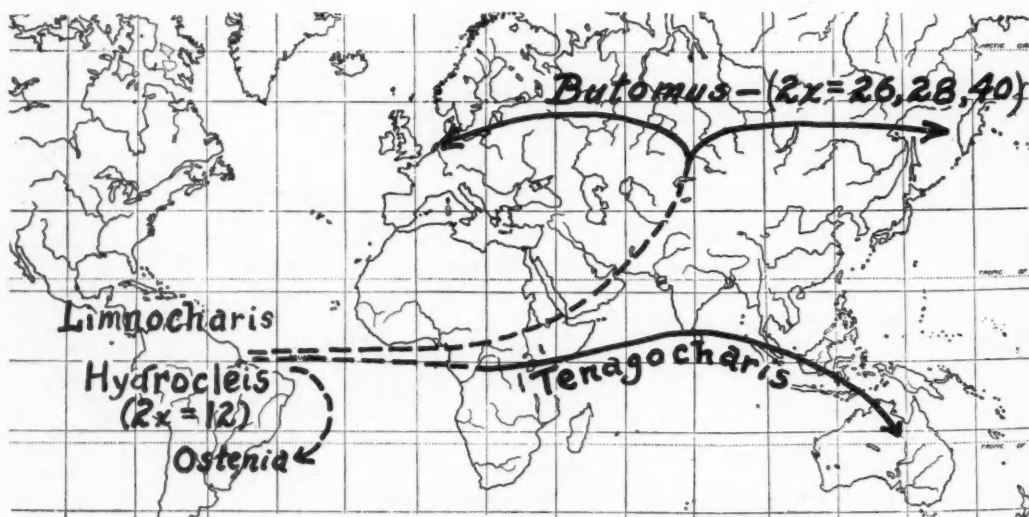


FIG. 24. Suggested phyletics and dispersal paths in the Butomaceae.

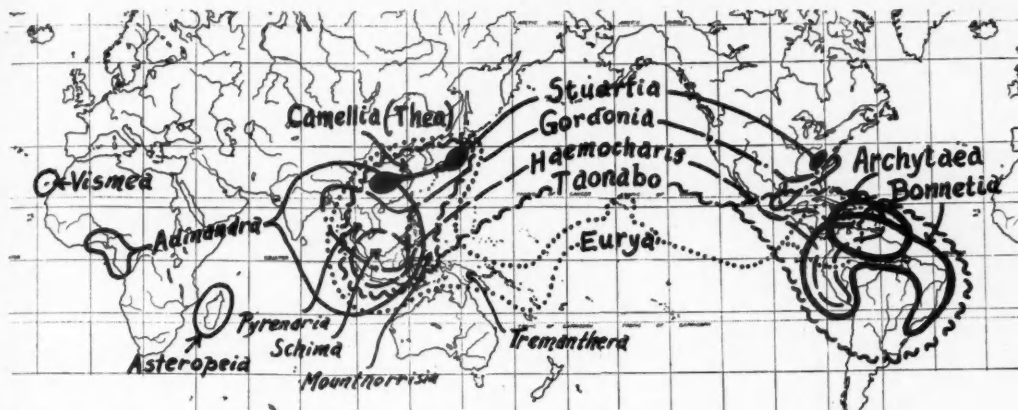


FIG. 25. Distributions of the genera of Theaceae. The genera *Stewartia* (a more preferred spelling than the *Stuartia* of the chart), *Gordonia*, *Haemocharis*, *Taonabo*, and *Eurya* are in eastern and southeastern Asia and also in either South America or North America. *Bonnetia* and *Archytaea* exhibit the more primitive characters among the living genera.

octoploid. In *Gaultheria*, three basic chromosome numbers are known, 11, 12, and 13. So far, the basic number of 11 is known only from the lower three-fourths of the "*Gaultheria* ring"; the 12 and 13 groups are in the upper (northern) part.<sup>6</sup>

Lacking space, I shall discuss only briefly the primarily South African genus *Erica*. However, certain students of this group tell us that the African species have been derived from the European members of the genus. Personally, I find such a viewpoint very

puzzling for it would mean that the European species, all of which have the highly advanced, whorled or cruciform, inrolled and marginally fused type of leaf, must, in some most remarkable manner, have given rise to the patently primitive, spirally arranged, non-fused, merely revolute margin-leaved South African species. It therefore would seem quite unlikely that Europe has been the original home of the genus *Erica*. The clue to its origin, perhaps, is to be found in the genus *Tepuia*, which has much to recommend it as an indicator of the probable appearance of what very well may have been the link between the primitive befaroid *Ericaceae* and certain of the lesser specialized *Ericas* of South Africa. These, in turn, show

<sup>6</sup> There is no intention here to intimate that the "*Gaultheria* ring" indicates the limits of the distribution of the genus; rather, it marks the general zone in which, in my opinion, the basic members of the genus are to be found, distributional outliers being present in eastern South America, to a slight extent in North America, and also in Asia.

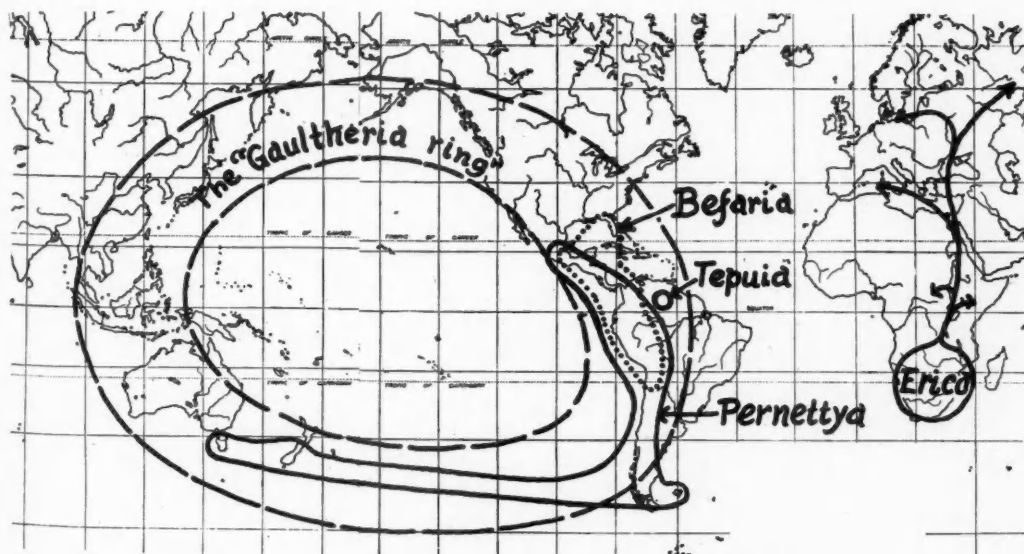


FIG. 26. Generalized distributions of a few genera of *Ericaceae*.

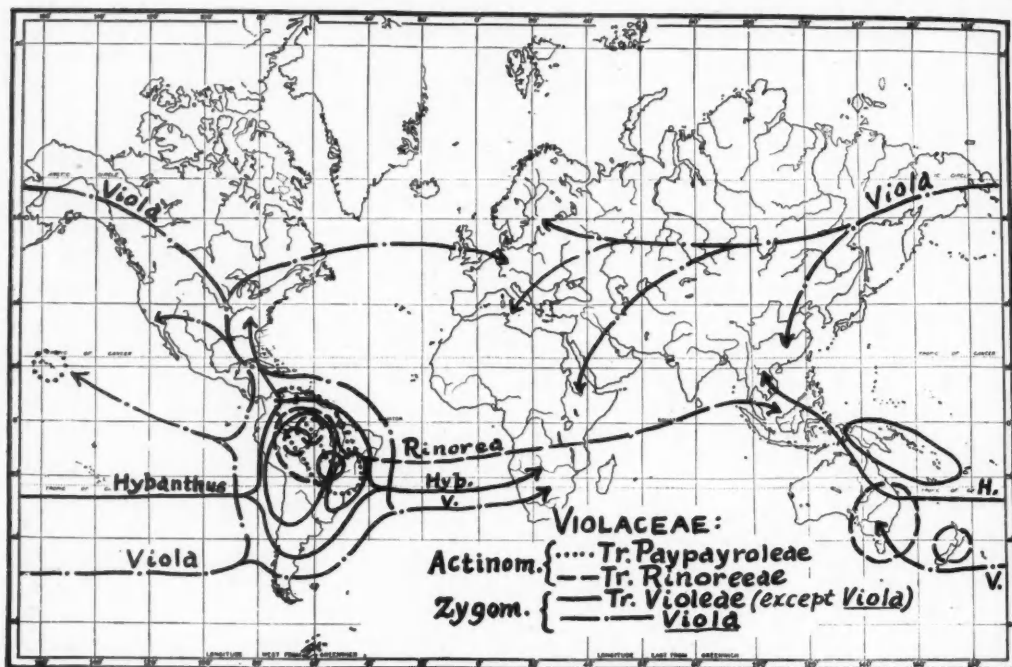


FIG. 27. Generalized dispersal pattern of the Violaceae.

every transition through the morphologically more highly advanced species of Africa to the species now in Europe. As yet, *Tepuia* is known from only one South American mountain. Who knows what surprises are in store for us when we really explore the remainder of these South American mountains, as well as the corresponding and but little known ranges which lift their cloud-swept heights out of the tropics of the West African coastal region?<sup>7</sup>

Would, also, that there were opportunity in this place to analyze the Violaceae in considerable detail (Fig. 27). Better yet, if it were possible, that we might all journey to the lowlands of South America and see for ourselves the primitive members of the family, living there as forest trees. Let us be clear about this: they are not primitive *because* they are trees; they are primitive because of a whole series of phyletically more important characters. As we examine them for divergences we see the general trends: tribe by tribe, genus by genus, and species by species, there is a steady transition, in South America, from these primitive arborescent members to the highly specialized genus *Viola*, with, as they ascend the evolutionary ladder, a greater tendency to achieve wider distributions. Also, in South America one can, in *Viola* itself, see the transition from shrubby forms, through subcandent types (I have seen them scrambling through shrubs to a height of

2 and 3 meters) to prostrate, rhizomatous perennial herbs and, ultimately, to annuals. The more highly specialized groups of *Viola*, while they have so to speak, one foot yet in the tropics, have already taken the necessary steps toward producing forms able to survive in cool-temperate regions. There on the slopes of the Andes, these groups have species which occur at high elevations on the bleak, bitterly cold and seasonally ice-clotted páramos. So far, even with its great galaxy of species in the Northern Hemisphere, the genus *Viola* has not produced a single life-form there which is not present in South America. I am therefore forced to conclude that the genus *Viola* was evolutionarily pre-conditioned, in South America, for its subsequent adventure into the Northern Hemisphere, as well as elsewhere.

#### SOME GENERAL OBSERVATIONS ON PRIMITIVE FORMS IN TROPICAL AND SOUTHERN REGIONS

If time permitted, I would analyze for you a series of paired families, such as we have here in the primarily tropical and woody Capparidaceae, and the usually temperate (or even arctic) and herbaceous Cruciferae (Fig. 28). Actually, if we are willing to face the facts, there is not a single good morphological gap separating these two groups. It is obvious, even with a little study, that the mainly herbaceous and often annual Cruciferae have been derived quite directly out of the tropical and sub-temperate, usually sub-perennial, herbaceous Capparidaceae.

So often in our great concern over those species

<sup>7</sup> Attention is here directed to a fairly recent paper which bears directly on this same problem:—C. Gilly, An Afro-South American Cyperaceous complex. *Brittonia* 5: 1-20. 1943.



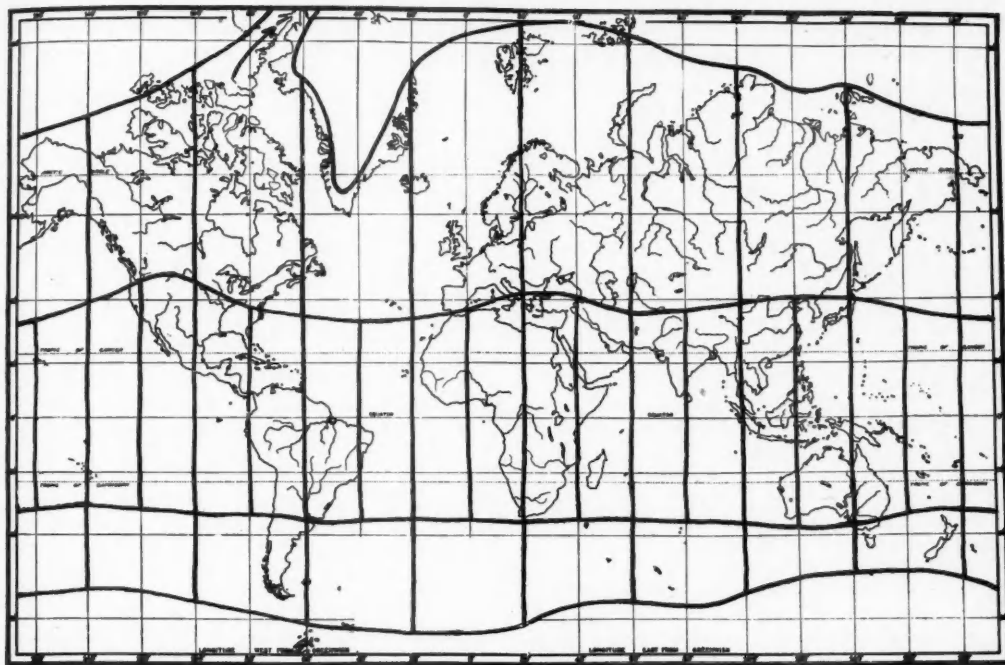


FIG. 28. Total-area distributions of the Capparidaceae and Cruciferae. The members of the Capparidaceae are essentially tropical, whereas the derived Cruciferae are mainly temperate, with some few forms in tropical and arctic regions.

which are about us and with which we are more familiar, we forget their real ancestors. If we wish to see the living primitive members of the Fagaceae—the beeches, oaks and chestnuts—in their native haunts we have to journey to New Guinea. The north temperate buckeyes and horse-chestnuts (*Aesculus*) with their zygomorphic flowers, tie directly into the tropical, capsular Sapindaceae by way of the actinomorphic-flowered *Billia* of Mexico. The mainly north temperate maples (*Aceraceae*)—beloved by the paleobotanists—are linked so directly with the tropical, samaroid members of the Sapindaceae that it is sometimes quite impossible on the basis of loose fruits (such as one might find in a fossil deposit) to tell to which family they belong. In the Tiliaceae, the morphologically highly specialized genus *Tilia* (the basswood, linden and lime-trees) is north temperate; the more primitive members of the family are tropical, with their phyletic roots in Australia, New Zealand, South America and Africa.

What is primitive in the Mimosaceae? Among its other characters would be a plant whose flowers bore numerous pistils and many stamens. This condition is found in the genus *Archidendron* with its numerous stamens and up to as many as 15 pistils per flower. The species of *Archidendron* are Australian.

The genus *Paeonia* (among which are found our garden peonies) is usually considered to be in the Ranunculaceae and, by many, is thought to be the

most primitive member of the family. Within the last few months, Corner,<sup>8</sup> and I think rightly so, has pointed out that *Paeonia* should not be considered a member of the Ranunculaceae; instead, it appears that both it and the Crossosomataceae have been derived from the tropical Dilleniaceae (Fig. 29). In this family one of the most generalized and, I think, primitive genera, *Tetracera*, is found primarily in Australia, Madagascar, South Africa and South America, with a few species extending northward into the American Antilles, Mexico and subtropical Asia. Thus, a careful re-analysis of phyletic relationships will often serve to reorient our approach to difficult problems; viewing them from a totally new aspect may even lead to concepts which, while disconcerting, are perhaps somewhat closer to the truth.

As an example of this, the question might be asked why I have not considered the Magnoliaceae in this discussion. Should the morphologists ever decide that the stipules of it and its sister families are not a primitive character but a secondary acquisition (and there are strong hints in that direction), then the whole question of the origin and relative placement of the Magnoliales would be laid open for critical re-examination. It is here suggested that any future study of the phylogeny of the perhaps not too primitive Magnolialean complex should be preceded

<sup>8</sup> Corner, E. J. H. Centrifugal stamens. *Jour. Arnold Arboretum*, 27: 423-437. 1946.



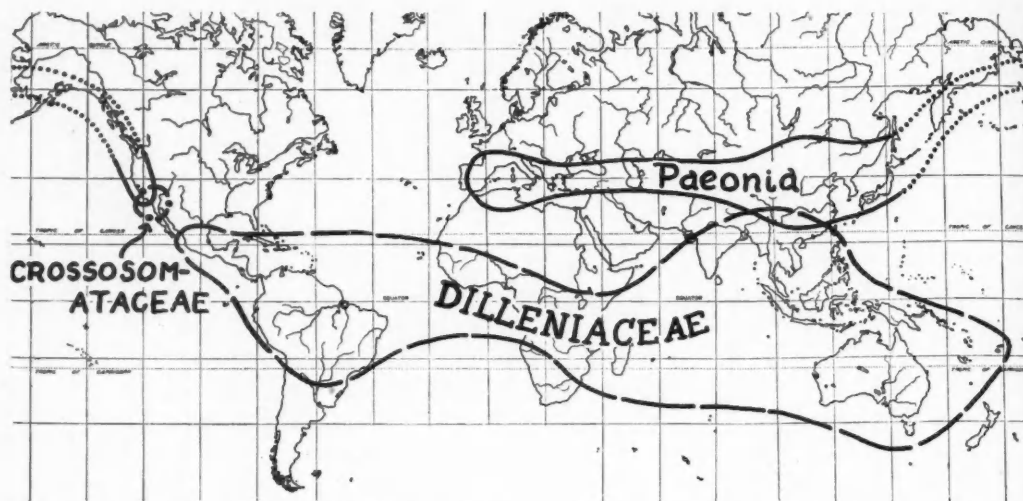


FIG. 29. Distributions of the Dilleniaceae and the probably derived Crossosomataceae and the genus *Paeonia*, this formerly placed in the Ranunculaceae.

by an examination of the Annonaceae. Certain characters of various groups of the Annonaceae are such as to recommend this family for careful consideration if we are seeking for primitive living forms among the woody angiosperms. It is needless to point out that, except for only a few species, the great Annonaceous complex is entirely tropical.

But, it could be asked: Where are those great Northern Hemisphere groups about which the taxonomist is always talking? Certainly some of their members must have migrated southward. For example, it has been suggested that, in the Grossulariaceae, we have such a group (Fig. 30). Now it just so happens that I have collected and studied in the field members of this family in North America, Mexico, Central America, and in South America, south of the Equator. I well remember the evening not so long ago in a little mud-walled hut high in the Andes while arranging some specimens of *Ribes* in the drying press, when the thought came to me that it was most remarkable, if the Grossulariaceae had arisen in the north (as I had long supposed), that only the relatively primitive forms had been eaten by birds (the usual biotic vectors of this group) and carried southward in their migrations.

For a long time this group has been rather well submerged (bibliographically) by association with the Saxifragaceae. Actually, the gooseberries and currants ought not to be so intimately associated with the saxifragas; they constitute a separate family and seem to be related to the Greyaceae of South Africa. In my estimation the Grossulariaceae are even more closely related to—and quite likely derived from—the mainly Southern Hemisphere Escalloniaceae (also bibliographic fugitives from the probably polyphyletic Saxifragaceae of the older systematists). Whether this now-compact group—the Escalloniaceae

and the probably derived Greyaceae and Grossulariaceae—belongs in the Cunoniales (as held by Hutchinson) is another question, which need not be discussed here. With this necessary and pertinent re-grouping before us, the whole picture of the present distribution of the Grossulariaceae becomes clarified and it no longer is a remarkable fact that the more primitive Ribesian members of the family "extend into" South America, there to become geographically associated with so many of the phyletically primitive members of the Escalloniaceae (some of which, both in the field and herbarium, exhibit astonishingly Ribes-like characters). It would seem likely that the Grossulariaceae originated in South America and have since spread northward.

#### "PRIMARY" vs. "SECONDARY" EVOLUTION

Perhaps what I have to say should end here. However, with the few data I have presented and the many questions I have raised, there is one more bit of data to lay before you and one small question to ask before I raise the final question. Perhaps I am a little old fashioned in my views; perhaps I am much too conservative. Nevertheless, I do feel that, with all our new techniques and ways of obtaining data and our various methods of statistical analysis, there yet remain certain obvious verities. And one of these is: the longer a group of organisms exists, the greater the opportunity it will have of carrying on natural "experiments" in evolution. As a corollary to this, it would seem obvious (at least to me) that a group which had arrived in a region comparatively recently would be less likely to have had time enough to produce derived and aberrant forms within the area than one which had been there much longer. On entering a new area speciation within a group likely would be speeded up tremendously. That phenomenon we can see in many groups. But we

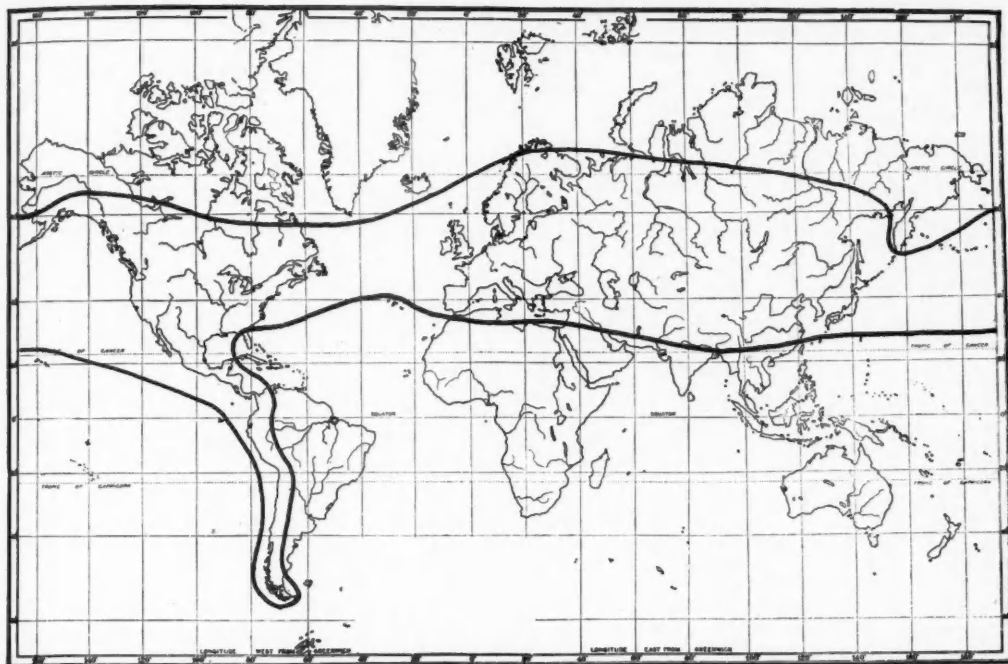


FIG. 30. Distribution of the genus *Ribes* (Grossulariaceae). The more advanced genus, *Grossularia*, appears to be entirely northern.

must not be confused in our thinking. Speciation is (what I choose to call) merely "secondary evolution" since, in plants, it is often accompanied by such phenomena as polyploidy and apomixis—both of which are naught but evolutionary blind alleys. "Primary evolution," the development of new types of organisms, is a very slow process indeed. It is so slow that only rarely (and provided he is fully acquainted with living floras) does the paleobotanist delving even into the Eocene deposits, have any great trouble in identifying his material, usually associating it with some modern genus. It is only when he gets back into the Cretaceous that his troubles begin.

#### AN OBSERVATION ON "DISTRIBUTIONALLY RESTRICTED" GROUPS

Therefore, for some time I have had the feeling that a study of the less aggressive (but nonetheless basic) primary evolutionary "experiments" of our living floras might, perhaps, shed some light on the area where the angiosperms have longest been occupying the land. Today we list about 300 families of angiosperms; of these 103, or one third, have fairly "restricted" distributions. (Among these I have included such as connect the Australo-South American and Afro-South American regions.) Here then, for the most part, and on the basis of their affinities, appear to be the "experiments" in the production of often "new" familial groups in the angiosperms—the basic evolutionary "trial balloons" of the flowering

plants. And where is the bulk of these "experimental" families? Are they mainly on the lands of the Northern Hemisphere? It would appear that they are not (Fig. 31). Five of these families are North American, with four of them actually subtropical. Four are Mediterranean, three of which have their roots in tropical Africa. That well known and much publicized connection across the old Bering Land Bridge, with its great series of bi-areal genera and paired species in temperate Asia and North America, yields us only five families. And the great temperate Asiatic flora, so uncommonly rich in genera and species, can show only a paltry six families, with several of these actually subtropical. The remainder of these 103 phylogenetically interesting families are primarily associated with the southern land masses, only rarely having sent a few species northward (see also Footnote 9, last sentence).

During the compilation of the material for this paper, it has become evident that, in the majority of instances, an analysis of a group indicates that the primitive members are in the southern parts of the group's range (with, of course, due allowance being made for those groups which have wide east-west and narrow south-north distributions). If we were to follow the well-known dicta of Matthews, we would conclude that these primitive forms were "driven" onto the southern land mass extremities by the more highly specialized, better adapted, and more recently derived groups of the north. The natural corollary

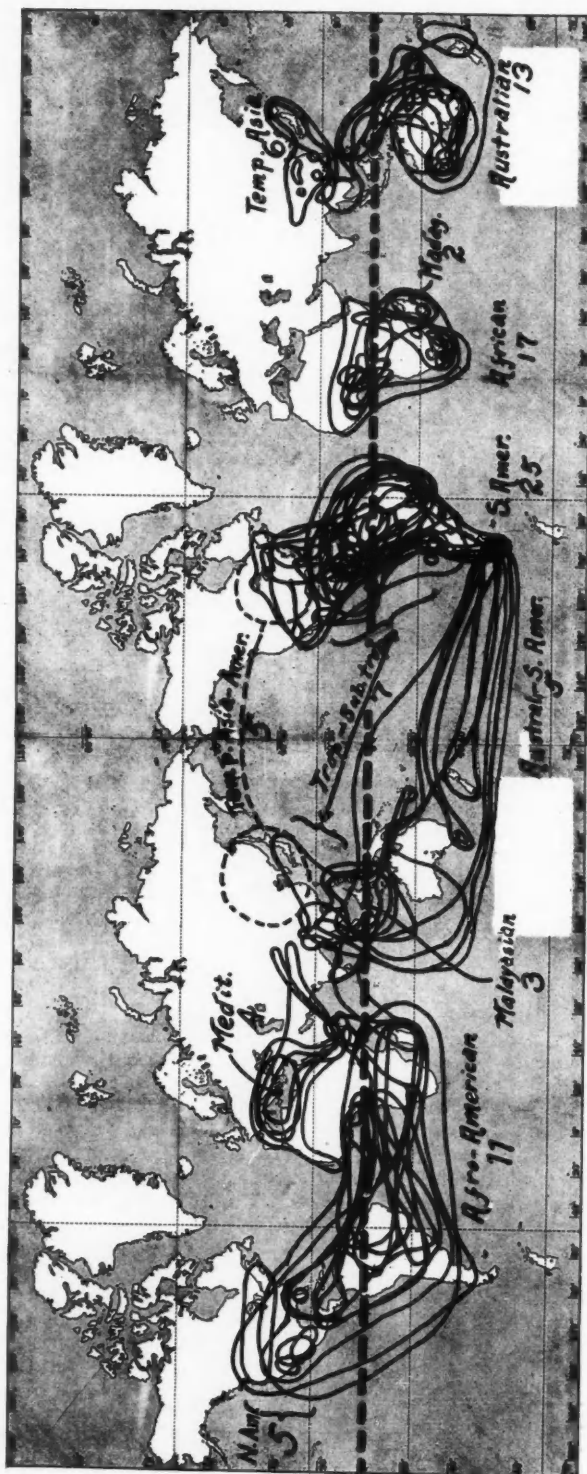


FIG. 31. Distributions of 103 plant families with "restricted" territories; that is, not wide-ranging as in the Cruciferae, Capparidaceae, and Theaceae.

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to this, therefore, is that we should find the majority of the peculiarly specialized and more recently derived families farthest away from the primitive forms. However, as can quite easily be seen, in the angiosperms, in most instances this is not the case. I therefore incline to the conclusion that these southern land masses are not only the original homes of the great majority of our basic angiospermous groups, but that also it has been on these same southern land masses where the greater part of their primary evolutionary divergences took place.

#### NEED FOR A BIOGEOGRAPHICAL BASIS IN PALEOGEOGRAPHY

There has been no opportunity in this discussion to wander afield, either from the assigned topic or into other spheres of investigation. Such groups as the Gymnosperms, which go back into the Devonian with but little break, offer their own peculiar problems; but these, basically, are no different from those which confront us in the Angiosperms; those who advocate a "bi-polar" origin of the Gymnosperms have much to explain. Recent investigations of various Cryptogamic plant groups indicate that they are not so universally distributed as has long been thought; these also will yield distributional information of a most pertinent nature. Also, personal discussions with various zoologists and paleontologists clearly indicate that there now are large cracks in the wall of stubborn resistance to a considerably different interpretation of their distributional and dispersal data than that which now is often so stoutly maintained in their published works. The temptation has been great to bring into the present discussion distributional items of a definitely parallel nature from the animal kingdom, if only to indicate that the problems of the zoogeographer are not too unlike those of the phytogeographer. Of necessity these items were left entirely to the zoologists to work out in their own manner. However, it would be hoped that it is not necessary to remind them that their animals are completely dependent on plants; that, of biological necessity, the true pioneers in any habitat, as well as its later primary stabilizing bio-factors, in any region, at any time, must be and always have been its plants. Therefore it would seem only logical that a true interpretation of zoogeography must be based on a correct understanding of phytogeography; it must be a BIOGEOGRAPHY. This must even be extended to the field of paleontology if we are to view the events of the past with anything approaching clarity. The whole subject of paleo-ecology is, as yet, scarcely touched. Such a combined attack will be needed before the field of paleogeography can be said to have been placed on a sound basis.

When workers in the field of paleogeography approach their problems from the viewpoint of biogeography the present variant interpretations will be resolved.

#### WHERE DID THE ANGIOSPERMS ORIGINATE?

And now for my last question. Throughout this discussion it has become increasingly clear that these southern land masses appear to be the possible areas of origin in so many groups; also, numerous close floristic connections between these same southern land masses have been demonstrated. Therefore, is it possible that, at one time, there might have been a more continuous land mass in the south than now exists?; a land mass sufficiently large to be capable of supporting a highly complex angiospermous vegetation, and that this was the real home of the flowering plants? Pressed for a place and date, I would say that it seems likely that the angiosperms, as a group, arose on this southern land mass contemporaneously with the Paleozoic of the northern (Holarctic) land mass and that the divergences of the basic, generalized familial groups had been accomplished on this southern land mass certainly by the mid-Mesozoic (Fig. 32A). The great bulk of the angiospermous families (at least their woody members) and many of their present-day genera, appear to have been evolved by the Cretaceous. It would seem evident also that, by the Cretaceous, our woody groups had become specialized to a point that they already had achieved a zonation which, in many ways, is the one they have preserved until the present. The presence, already in the Cretaceous, of highly divergent groups with a remarkably "modern" aspect, as well as an advanced physiological reaction resulting in phytogeographic zonation, is the primary reason for placing the origin of the angiosperms at a somewhat earlier date than is customary.

As Dr. Chaney points out in his paper in this symposium, the assemblage of genera in the North American Cretaceous was quite "modern" in its general aspect (although I feel emboldened to suggest that the majority of the species appear to be somewhat generalized and primitive with respect to the modern ones). However, possibly as a result of an amelioration of climate, the basic phytogeographic zonation, already well on its way to complete establishment in the Cretaceous, began moving northward so that by the Eocene at least subtropical genera became abundant on the lower parts of the northern land mass (Fig. 32B). This general northward movement of the basic vegetation zones appears to have continued into the Oligocene. Figure 32C, in a generalized and quite crude manner—and with admittedly many possible variations and much-needed modifications—may be taken as representing something of the situation in the Oligocene. In this figure there has been no attempt to delimit the various vegetation zones on the northern land mass; nor has any attempt been made to indicate the later Tertiary history of these zones, these items being outside the scope of the present paper. However, I do feel strongly impelled to re-affirm my contention that I see no evidence in the available data to indicate that



this northern land mass necessarily has been the original home of the basic angiospermous groups; that the obvious post-Oligocene southward movements of our North American Tertiary floras is *not* the result of "population pressure" on the older floras by newly developed and more aggressive types. Instead, it appears only to be a reversal of the former northward migration of the characteristic floristic groups associated with normal vegetation zones, this reversal of migration induced by climatic deterioration on this northern land mass during the later Tertiary.

The causes back of this seeming "climatic deterioration" on the northern land mass is quite another problem. Perhaps it may yet be demonstrated to be the result, in part at least, of a northward continental displacement resulting in an apparent southward migration of the superposed floras, these still maintaining their relative positions in the normal, broadly defined, climatic belts. A discussion of the problems relative to the presence of fossil forest species in the Arctic is somewhat outside the bounds of my topic, but not of this symposium. For example, Just (this

symposium, under the subtopic: Centers of Origin and Dispersal; and Summary, paragraph 3) holds to a northern origin of the angiosperms, basing his arguments on the usual data as well as evidence that, today, such genera as *Platanus*, *Ginkgo* and *Sciadopitys*, as transplants, can "withstand the coldest winter in Europe." Dr. Just neither tells us what part of Europe it is to which he refers, nor does he state the northern limits of these genera in cultivation; certainly he does not mean that part of "Europe" north of Latitude 65 degrees. With considerably amplified data, Chaney (this symposium, under the subtopic: The Arcto-Tertiary Flora) also discusses this situation, expressing essentially the same viewpoint regarding possible conditions in the Arctic. The mere fact that both these participants in our discussion saw need to justify the hypothesis which they follow clearly indicates that a real problem exists. The biological problems inherent in the existence of extensive forests in high latitudes have been so ably discussed by Mason (this symposium, under the subtopic: On Northern Origins and the

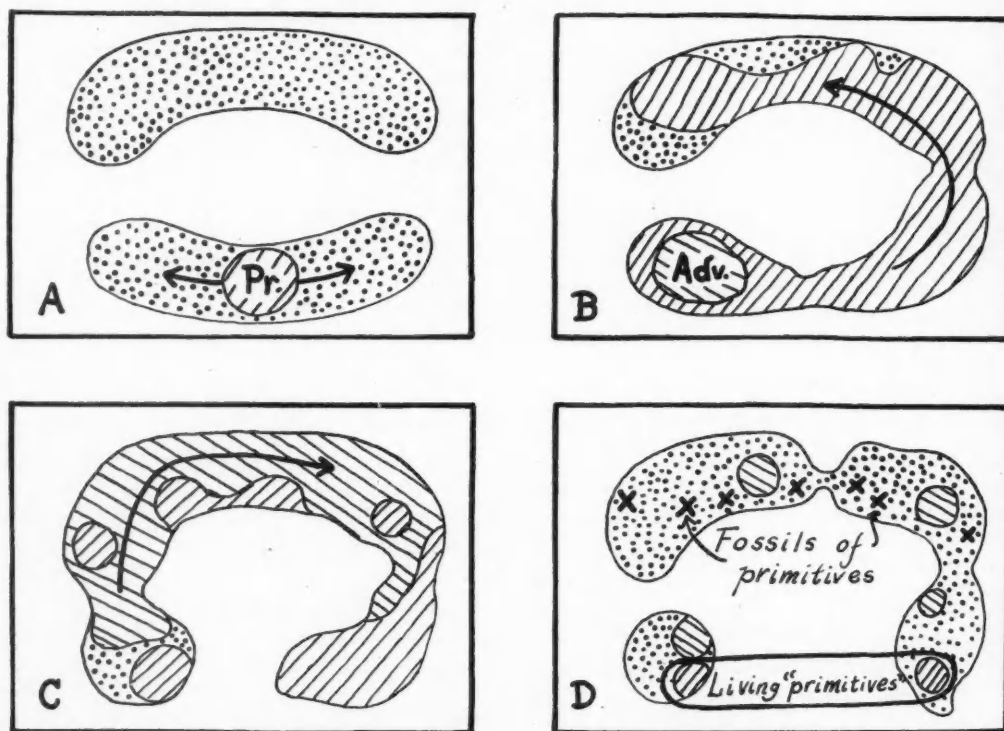


FIG. 32. Proposed history of a hypothetical angiospermous group. (A)—the primitive members—Pr.—arose on a southern land mass; (B) as opportunity afforded they spread onto a northern land mass by way of newly made land connections; subsequently, advanced members—Adv.—arose out of the relatively older of the primitive stocks; (C)—with another connection then available, those advanced members also spread onto the northern land mass where, because of possible climatic changes, the former primitive members were disappearing or had disappeared, leaving only fossil remains; (D)—after further topographic and climatic changes took place on a worldwide scale, there are at present on the northern, now partly segmented land mass the fossils of the primitive members together with living advanced members; on the remaining segments of the former southern land mass are to be found relic members of the more primitive types of the group as well as living advanced members. Many variations of the foregoing could—and probably did—occur. This should be compared with Figure 5.



Permanence of Continents and Ocean Basins) that I see no need to amplify them here.

### CONCLUSION

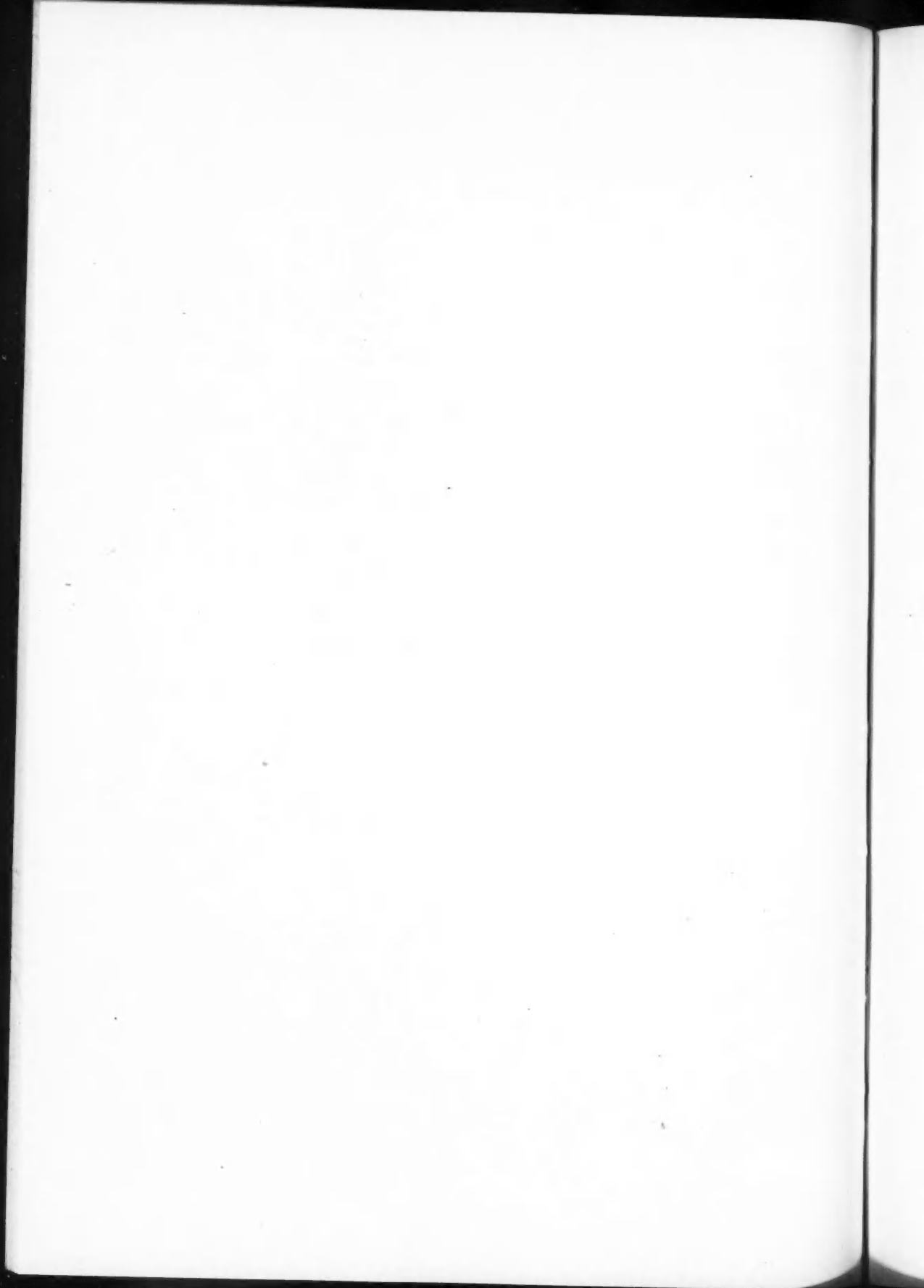
As mentioned, it has not been my task in this symposium to examine the Tertiary history of our angiospermous groups; mine has been only to trace some of the characteristic distributions encountered in living floras, many of them with exceedingly interesting and provocative patterns. A study of these patterns (and many others necessarily omitted here) has led me to the conclusion that the southern land masses have been much more important centers of primary familial evolution in the angiosperms than is usually accorded them. I therefore offer for your serious consideration the hypothesis (it is by no means original with me) that the present distributions of fossil and living floras can be accounted for on the basis of a southern origin with no greater complications than that which demands a northern origin, this latter view being one which, for so long, has been influencing our thoughts and conclusions. Certainly, in my opinion, a study of distribution patterns in relation to basic phyletic phenomena points rather directly to a southern origin of the angiosperms.<sup>9</sup>

<sup>9</sup> Since this was written Croizat (Torrey Bot. Club Bul. 74: 60-76, 1947), in a study of *Trochodendron*, *Tetracentron*, and other angiosperms (p. 63) has stated: "It is plain . . . that the Cornaceae and Saxifragaceae—not to mention other families necessarily omitted—are bound by clear phylogenetic ties not to 'holarctica' but to the southern hemisphere. *This indeed is the case with an overwhelming majority of the angiospermous families.* . . ." [The italics are mine.] He continues (p. 64): "Suffice it to say that a typical Sino-Himalayan family like the Lardiz-

Naturally, such a sequence of events will demand a former somewhat different (but I think geologically not impossible) alignment of the land masses of the Southern Hemisphere than now exists. However, that need not trouble us greatly for much the same situation, if we face it squarely and without hedging or equivocation, is true of the entire problem of ancient biotic dispersals, even of such local areas as the Caribbean or, for that matter, the old Bering Land Bridge. The problems of geomorphology and paleogeography are yet far from being solved. Possibly a really critical study of present-day angiospermous dispersal patterns—going far beyond the one presented in this cursory discussion—will direct some rays into the dark corners of this perplexing problem. The details of a solution are as yet obscure, but I do believe there is more than a mere glimmer of light ahead.

This light, however, does not come from the north polar region. The answer to our riddle will not be found in studies limited to materials of the northern continents; rather, we must seek for its solution in lands far to the south. There is no escaping the conclusion that the great majority of the components of our northern floras have their phyletic roots in the ancient lands of the southern hemisphere. It was from tropical and southern archetypes that our northern angiospermous forms descended; it was of such elements that the associated groups in modern floristic areas were compounded.

balaceae has two genera wholly isolated in Chile, which should readily give pause to hasty speculations about the 'holarectic' origins of forms now appearing as 'relics' in the Far East."



CHARACTERISTICS OF NATURAL AREAS AND  
FACTORS IN THEIR DEVELOPMENT

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IN A SYMPOSIUM ON  
ORIGIN AND DEVELOPMENT OF NATURAL FLORISTIC AREAS  
WITH SPECIAL REFERENCE TO NORTH AMERICA

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# CHARACTERISTICS OF NATURAL AREAS AND FACTORS IN THEIR DEVELOPMENT

## INTRODUCTION

The subject which I have been invited to discuss is one of such magnitude that I enter upon it with some trepidation. The title of my contribution is almost that of the symposium as a whole, and each other member will treat the subject according to his views and the restrictions of his particular field. Not dealing with any one type of vegetation or region, or with such matters as dispersal, migratory routes, and geological history in a specific manner, I shall select a few points which seem to me to be significant, often understressed, and perhaps a little different from the point of view of many ecologists and plant geographers.

After outlining the nature of the types of areas that have been mapped in the field of interest of this symposium, and presenting a very brief consideration of the types of factors operative in the development of areas, I shall: (1) attempt to show a close relationship between floristic and vegetational phytogeography, (2) bring into question the objective reality of the plant association, and (3) emphasize the employment of natural areas conceived in terms of collective data of many sorts, rather than from single factors or single points of view.

## TYPES OF MAPPED DATA OF INTEREST TO BIOGEOGRAPHY

This symposium treats of natural floristic areas, but it is no simple problem to ascertain what is a natural area. Most of my remarks are related to this problem. Biogeographers have depended heavily upon data mapped by physical geographers and have contributed some maps of their own. The next few paragraphs suggest briefly the variety of kinds of areas with which biogeographers deal. These data are given here at the beginning of my discussion merely to emphasize that it is always necessary to define one's point of view and purpose when speaking of natural areas.

The types of data which have been mapped are suggested by the outline in Table 1. This is not a complete list, nor is it a classification of all mappable data that might be pertinent. Neither would I follow those geographers who say, "If it isn't mappable, it isn't geography."

One notices immediately that the data are of different orders of completeness and the maps, consequently, of exactness, even when the maps present the most modern information. This is inevitable from the nature of the subject. Nevertheless, even the more elusive types of data and the more complex integrations can be given a degree of exactness on large-scale maps that is commensurate with the con-

TABLE 1. Types of map data of interest to or produced by biogeography.

Types of data	Examples
<b>PHYSICAL DATA</b>	
Geological areas	
small-scale maps	Many U. S. Geol. Surv. publ.
large-scale maps	Many U. S. Geol. Surv. publ.
Geomorphological areas	
physiographic areas	Fenneman, 1916
physiographic diagrams	Raisz, 1939
contour maps	U.S.G.S., T.V.A., etc.
Soil areas	
small-scale map	1938 Yearbook, U.S.D.A.
large-scale maps	Many Soil Surv. publ.
Climatic areas	
climatic types	
Köppen system	Ackerman, 1941
Thornthwaite system	Thornthwaite, 1931, 1938
climatic years	Thornthwaite, 1936
single climatic factors	
vapor pressure deficit; rel. hum.	Huffaker, 1942
isotherms, isohyets, etc.	Brooks, 1936
<b>BIOLOGICAL DATA</b>	
Faunal and floral areas	
faunistic areas	Wallace, 1876
floristic areas	Hayek, 1926
Vegetational areas	
formations	Weaver & Clements, 1929; Brockmann-Jerosch, 1930
associations, assoc. groups	Shantz & Zon, 1923
forest types and cover types	Many For. Serv. publ.
Biotic areas	
provinces	Dice, 1943
biome	Carpenter, 1940
Agricultural areas	
crop types	Klages, 1942; U.S.D.A. publ.

cepts involved. Both small and large-scaled geological maps of a well studied region have considerable accuracy, and the interpretations of different geologists, say of adjacent states, produce maps of close conformity. Topographic maps also can have great accuracy, especially with the improved methods of aerial survey. Soil maps are dependable and, during recent years and in a single country, comparable because of the standardization of classificatory characteristics. Maps of climatic data, in contrast, are much more diverse. The mapping of climatic regions and areas in the first place depends upon the selection of and formulae for the integration of climatic data and, consequently, becomes a somewhat personalized process. This is illustrated by a comparison of the revised Köppen climatic map for North America (Ackerman 1941) with that produced by Thornthwaite (1931). Maps of climatic types are usually based upon some combination of precipitation and temperature data. In addition to such maps, there is a large series of maps which portray separately data for certain of the climatic factors or ele-



ments. Without listing all of the examples which are available, the following are suggestive: snowfall, snow duration, seasonal distribution of precipitation, length of frost-free period, evaporation, relative humidity, saturation deficit, isotherms, isohyets, isobars, etc.

The biologists also have been engaged in mapping data from their fields, and their results can be classified into at least four groups showing faunistic and floristic, vegetational, biotic, and agricultural areas. The maps of floristic and faunistic areas are of two types. First there are those which portray the areas of individual species, genera, or other taxonomic units. The treatment is either generalized or on a basis of spot occurrences. Also there are the maps of the kingdoms, regions, provinces, etc. which are supposed to portray the essential faunal and floral characteristics of areas and regions as a whole. Vegetational maps are somewhat more modern than floristic maps in as much as ecology is a newer science than taxonomy. Such maps show the formation types, associations, forest types, etc., and they are a very heterogeneous group because of the inadequate factual basis for most of them, and because ecological philosophy plays such an important role in the concepts of the communities which are mapped. Biotic maps present information on the biome as understood by Shelford and others, or are of the type represented by Dice's "Biotic Provinces of North America." Maps of agricultural areas are as a rule the most accurate of the biological maps because of the usually large mass of quantitative data upon which they are based. Although showing the areas of single crops or of groups of closely related crops, agricultural maps often represent natural areas and an integration of data concerning numerous environmental factors, especially climate and soil.

#### INTERDEPENDENCE OF MAPS

It is important to emphasize the interdependence of maps. What I mean is that map makers who are interested in expressing information upon a certain subject are very likely to be influenced in the drawing of the position of boundary lines by the position of boundary lines which others have drawn on maps presenting different natural phenomena. For example, in the preparation of a small-scale vegetational map the investigator often if not usually makes use of pre-existing maps of the climatic types, topography, soils, and agriculture of the region under consideration. This is natural because of the prevailing shortage of information on the vegetation, *per se*, and because of the realization that vegetational areas do have some close if poorly defined correlations with the environmental factors. It should be recognized and kept in mind, however, that this interdependence of maps may result in the perpetuation of mistakes and some very rough approximations of the truth. The ideal is for a map to have an objective basis solely in terms of the type of data being mapped. For most regions and subjects this is a goal rather than a realizable actuality. It is also true that when

one attempts to map natural areas on a basis of total characteristics, rather than on a basis of single factors, it becomes impossible to draw boundaries with any degree of accuracy except for the smallest natural areas when mapped on a very large scale.

#### FACTORS IN THE DEVELOPMENT OF NATURAL AREAS

Maps of natural areas are usually attempts to portray the interplay of historical and contemporary environmental factors or complexes and the areas of occurrence of the affected biotic phenomena. The factors which play a role in the development of natural areas fall into two divisions: factors which are now operative and those which have been effective in the past. The only difference between these two groups of factors is the time element, but there is a vast difference in the method of studying them. Present day factors operative in the determination of natural areas are more or less subject to direct observation and often to some degree of measurement, and their relations to living organisms are subject to experimental approach and verification. Historical factors are only examined by inferences based on the assumption of the past operation of factors in manner similar to their operation today. The first is subject to direct inquiry, the second to indirect inquiry.

The foregoing discussion of the types of areas which have been mapped is suggestive of the nature of the factors which produce natural areas. They are the various and numerous geological, geomorphological, edaphic, climatic, biotic, catastrophic, and human agencies and influences. Unless one arbitrarily limits his attention to a single factor or to a restricted group of factors—and so limits his basis for definition and delimitation of natural areas—he is confronted with the necessity of a more or less subjective delimitation of natural areas. What I mean is that the number of operative factors is so great, and the mutual effects and interrelations so complex, that the investigator must decide somewhat on the basis of how he feels about the matter just where the boundary of a particular area is to be recognized. This is in the nature of things and not to be decried, but it does place a heavy burden of responsibility upon the map maker (or one who deals with the subject, whether or not he has the temerity to draw a map), and gives the cloak of authority only to the scientist with wide experience, broad knowledge, and that imponderable which may be called good biological sense.

I wish to say plainly that no amount of physical data, however accurate, detailed, and widespread can ever suffice without the opinion of an experienced field naturalist in solving the problem of natural areas. The primary data must be the plants and animals themselves and the communities which they form, with physical data on climate, soils, etc. falling into a subordinate place. I do not mean to say that good environmental data of a physical type are not useful, for they result in many interesting and prob-

ably significant correlations with biological phenomena; and certainly abundant and exact biological data are requisite in the determination of natural areas; but above all it is the role of naturalists to interpret nature. In view of the complexity of any environmental situation, large or small, and in view of the drastic limitations to the analytical method whereby one gains information about the single factors, the synthesis of the individual types of data back again into a whole seems to be a mathematical impossibility. It follows, then, that the exercise is an intellectual one of a different order from everyday physics, chemistry, and mathematics. I will not say that this type of ecology is an art, but it is something less than an exact science.

Ecology and biogeography during recent decades have become enamored of physical data. As a consequence there is a surprising paucity of information on the exact areas of species (this field having been left almost wholly to taxonomists) and particularly on the composition, structure and total areas of plant communities. I refer not to the hypothetical and admittedly approximate areas of "association types," according to the concepts of Clements, for example, but to actual, concrete, specific communities on the ground. One way of explaining what I mean is by reference to the difference between a cover-type map (as used in the sense of foresters to show actual vegetation) and an associational map, as often presented by ecologists, purporting to represent climates. The former objective type of map is needed by plant ecology and geography. The latter may or may not result when abundant objective data are available.

Natural areas have existed in the past, in some cases through geological lengths of time in about the places where they are now found; in other instances there have been extensive migrations of natural areas under the influence of geological changes and climatic compulsion. At more ancient times there must have been other types of natural areas on the earth's surface than now exist, if for no other reason than the fact that the flora and fauna were different.

It is certainly true that any natural area which one wishes to study can not wholly be understood in terms of present day conditions. There are always aspects of the communities, and of the component fauna and flora, which can be understood only in the light of past evolution and migration. And these, in turn, are related to past changes in geology, climate, etc. (Cain 1944, Chaney 1940, Clements 1934, Engler 1879, Gleason 1923, Wulff 1943).

Paleobotanists have gained immeasurably in understanding of past vegetation and conditions, as have ecologists of present-day vegetation, through the employment of the techniques of paleoecology, yet this is a field fraught with hazards for the unwary investigator. One example will suffice. There is some pretty good evidence for the occurrence of rather widespread, Tertiary, mixed-mesophytic forests, but

this does not warrant the assumption that the whole deciduous forest was without differentiation into associations. At no time in the history of vegetation has there been an absence of climatic gradations related to latitude, altitude, and continentality, or of floristic areas of some degree of differentiation. It is true that paleontological data provide evidence for former vegetation types being more mixed (in the sense that today many of their elements are extinct, segregated on different continents, or in different natural areas of one continent), but it also is true that some of this apparent mixed condition is not proven, especially as to its geographic extent at any one time in geological history. Tens of thousands of years of vegetational history are often telescoped into one time unit, which is not long for Tertiary history or even Eocene or Miocene history, but is long in terms of potentialities for vegetational migration. In the simplest cases, the "mixed vegetation" may merely be mixed depositions from different locally segregated types of communities. I believe there is much to the idea of the Tertiary mixed mesophytic forest and the historical segregation of associations from it, as interpreted by Braun (1935a, and later dates; also this symposium). It is obvious that she never conceived of the Tertiary deciduous forest as being without associations or segregates. For many other authors, however, the Aretotertiary forest is apparently conceived as an homogeneous whole.

## DELIMITATION OF NATURAL AREAS

### FLORISTIC PHYTOGEOGRAPHY

The idea of natural floristic areas in the plant life of the world was an early development in botany that resulted as the geographic reports of travellers and the accumulation of collections in herbaria became abundant. The floristic characterization of geographic regions is an ancient and honorable practice, as exemplified by Linnaeus' "Flora Lapponica" in 1737, and taxonomists and geographers are still busy with that problem and the determination of the areas of occurrence of individual species, as shown by the frequency in the literature of such titles as "Additions to the flora of Indiana," "Polynesian plant records," etc. It soon became apparent that plants are not indiscriminately distributed, that each species has a definable area, that there are pattern types for the areas of different species, and consequently areas that are characterized by a greater or lesser number of endemic species. Such natural floristic areas range in size from very local ones to ones that have a certain unity although they occur on two or three continents.

Willdenow (1811) believed that every major mountain mass had its peculiar flora and that there are as many chief phytogeographical kingdoms as there are primitive mountains. Schouw (1823) delimited 18 floristic kingdoms to which he later added nine more. These kingdoms were in some cases di-

vided into provinces, as shown by the following example:

Kingdom of Saxifragaceae and Musci (Alpine-Arctic flora)  
Province of Carex (Arctic flora)  
Province of Primulaceae and Phyteumae (Alpine flora of the south of Europe)

Schouw laid down certain rules for the determination of floristic kingdoms and provinces. He said that a kingdom must have: (1) at least half the known species of that portion of the globe peculiar to it; (2) one-fourth of the genera peculiar to it or so prevalent there that they do not represent another region; and (3) families that are restricted to or reach their maximum of development in it. The kingdoms can be subdivided into provinces when a certain area has one-fourth of its species peculiar to it and at least some peculiar genera. Meyen (1836) noted that Schouw had not followed his own rules in setting up kingdoms and that by a similar loose procedure many more kingdoms could have been erected. Drude (1884) recognized 14 floral kingdoms and 55 regions and established the following hierarchy for the classification of floristic territories:

Florenreichsgruppen  
Florenreichen  
Gebieten  
Bezirken  
Landschaften

Modern floristic areas, or rather the designation of them, as represented by the opinions of Engler (1879, 1903), Rikli (1913), Diels (1918), Hayek (1926), and others, all have a considerable similarity and are well represented by the classification of Engler and Diels (1936) in the 11th edition of the "Syllabus der Pflanzenfamilien." There are only four kingdoms for all terrestrial vegetation (I. Northern Extratropical or Boreal Kingdom—Holarctic. II. Paleotropical Floral Kingdom. III. Central and South American Floral Kingdom—Neotropical. IV. Southern or Old Oceanic Floral Kingdom.). These are subdivided into 29 regions, and the portion of the classification that pertains to North America is shown in Table 2. These authors have followed Harshberger (1911) closely in their delimitation of American floristic areas.

The early students of floristic geography were not long in arriving at certain generalizations regarding floristic areas and the increase or diminution of certain families in equatorward and poleward directions and what they called the laws of plant geography, and every decade has seen efforts along these lines (Pickering 1876, MacMillan 1892, etc.). As early as 1819 Winch referred to the then recent progress in plant geography being made by Wahlenberg, von Boeh, De Candolle, and Humboldt, and he, in producing the first plant geographical study in England, classified the 2,176 species of three counties according to such characteristics as whether they reached northern or southern limits in the district. Rare plants were grouped according to whether they are native

TABLE 2. The floristic territories of North America according to the classification of Engler and Diels, 1936.

I. Northern Extratropical or Boreal kingdom	
A. Arctic region	
1. Arctic province	
c. Subprovince of Bering Sea lands and western Alaska	
d. Arctic North America and northern Labrador subprovince	
e. Greenland subprovince	
B. Subarctic or conifer region	
3. Subarctic American province	
a. Southern Alaskan subprovince	
b. Peace and Athabasca river land subprovince	
c. Northern Ontario subprovince	
d. Quebec and Labrador subprovince	
H. Pacific North American region	
1. Pacific conifer province	
a. Northern subprovince	
(1) District of northern Coast forest	
(2) Cis-Cascadian forest district with Cascade Mts.	
b. Southern subprovince	
(1) California Coast forest district	
(2) Western Nevada forest and Sierra Nevada district	
2. Rocky mountain province	
a. Northern subprovince	
b. Central subprovince	
c. Southern subprovince and transition to the chaparral-Sonoran province of Central American xerophytic region	
3. Western American Desert and Steppe province	
a. Subprovince of transition to the chaparral-Sonoran province in the Gila and Mohave deserts	
b. Subprovince of the Great Basin	
c. Inner California subprovince	
I. Atlantic North American region	
1. Lake province	
a. Pinus Strobus subprovince	
b. Eastern transition subprovince with the summergreen forest	
2. Province of Mississippi and Alleghany forests with the Alleghany Mts.	
a. Mississippi-Ohio-Tennessee subprovince	
b. Alleghany subprovince	
c. Pine-barrens subprovince	
3. Evergreen province of South-Atlantic states	
a. Subprovince of Coastal swamp conifers	
b. Mixed forest subprovince	
c. Prairie-woodland subprovince	
d. Northern pine forest subprovince	
4. Prairie province	
a. Northern subprovince	
b. Central subprovince	
c. Southern subprovince	
III. Central and South American kingdom (Neotropical)	
A. Middle American xerophytic region	
1. Chaparral province	
2. Sonora province	
3. Province of Mexican highlands	
B. Tropical American region	
1. Province of tropical Central America and southernmost California.	
a. South-Californian subprovince	
b. Mexican subprovince	
c. Yucatan subprovince	
d. Guatemalan subprovince	
2. West Indian province	
a. South Florida, Bahama Island, and Bermuda subprovince	
b. Cuba subprovince	
c. Jamaica subprovince	
d. Santo Domingo subprovince	
e. Puerto Rico subprovince	
f. Lesser Antilles	

of Switzerland, Lapland, or both, or some other place. Maritime plants were subdivided according to whether they were confined to coastal areas, or extended also from sea-level to 2,000 feet altitude, or were disjunct from the coast to high mountains. Taken al-

together, Mr. Winch sounds quite like many twentieth century students of floristics and was close to the concept of "floral elements," which was first introduced into plant geography by H. Christ (1867). But such rules for the definition of floristic territories as were now and then promulgated seem never to have been slavishly followed, and the botanists who have known most about the distributions of plants have defined floristic areas according to less objective methods and have let the mathematics go.

If that sounds like an aspersion, I do not mean it so, for I do not believe that the materials permit a standardized and mechanical procedure. However, as information increases there are certain techniques which can be employed that are partly objective. A sort of statistical procedure is sometimes necessary as Lam (1945) has just emphasized in his study of the geographic elements in the Celebes flora.<sup>1</sup>

Floral territories have usually been delimited by approximation and selection of species. In the early days of floristic phytogeography and in preliminary studies on any region such methods are all that can be employed. As a matter of fact, certain approximations can never be avoided in the delimitation of floristic areas; but there is a method referred to by Lam, described by Gaussen (1933), and employed by Raup in this symposium, which is without the "mumbo-jumbo" of arbitrary rules. Gaussen wrote that if one superposes the limits of areas of a large number of species on a map, one finds that numerous limits fall in the same place. One can thus delimit the domains of greater or lesser extent, characterized by the exclusiveness of a number of plants. The method can be extended to the mapping of genera and families.

The first step is the preparation of as accurate spot maps as the available collections permit. Next the area of a species is bound by a line drawn around the peripheral spots of known occurrence. The area should not be extended beyond the limits of known occurrence by employing any assumptions which depend upon physiographic, climatic, or soil boundaries, for the mapping should be as objective as possible and depend solely upon floristic data. Outlines having been prepared of the areas of the species, they are superposed on a single map or, if the number of species is large, those whose real limits suggest a floristic territory or boundary line can be placed together on one map and those determining other boundaries on other maps. This is not at all the same procedure as the subjective selection of a few species to represent a floral territory, for all species are employed.

I believe that this method of determining floral boundaries and of classifying the floristic elements in the flora of a local area is the most satisfactory

one yet devised by geographers. But it has serious draw-backs. Large numbers of species must be dealt with—the whole flora under consideration—and spot maps have been published for comparatively few species. Also, taxonomic questions will always arise to plague the geographer. The floristic plant geographer needs access, then, to large plant collections and library resources.

A correlative problem is even more difficult to handle. How is the geographer to indicate differences in abundance within the area of occurrence? This question is of importance for the ranges of species, and of even greater significance in generic and family areas. For example, certain tropical families have only an occasional temperate species, and yet this one species in a hundred grossly enlarges and really falsifies, for these purposes, the area of the family as a whole.

Reference has been made to the term "floral element." This idea will be expanded slightly because any natural area of even moderate size, defined by any criteria at hand, will be found to contain some "extraneous elements" (Cain 1930) which are considered to be more characteristic of other areas than the one under consideration. The study of floral elements within a flora or the vegetation of some area is primarily a means to aid an understanding of the historical development of the area. Floristic studies of the history of natural areas are not only aided by paleontological data, but paleontology itself becomes involved in the floristic problems of extraneous elements in a fossil flora and its still earlier history.

Originally the concept of element had only a geographic significance, but Engler (1879, 1905) modified the term to indicate center of origin and direction of migration. Braun-Blanquet (1919, 1923) proposed restoring the term to its original purely geographic significance, but with the elements based on the phytogeographic regions as determined by Flahault. In a recent paper on the floral elements in The Netherlands, Heimans (1939) criticized the proposal of Braun-Blanquet although he likewise favored the use of the term element in a purely geographic sense. Heimans concluded that the only practical method is to define the elements of the native flora of an area in relation to the area being studied, and not to some supposed universal system of floristic regions. This point of view, with which I wholly agree, results in Heimans proposing such simple and straightforward definitions as the following: "The boreal element of our flora contains the native plant-species the centre of whose area lies distinctly north of us, so that they reach or approach their southern limit here with us."

#### VEGETATIONAL PHYTOGEOGRAPHY AND BIOECOLOGY

In the preceding section attention has been given to natural areas of the floristic type and it is apparent that what was referred to are the species without reference to their organization into communities and vegetation (Tansley and Chipp 1926). As Egler explains (1942), there are five emergent wholes in which

<sup>1</sup> Lam wrote, "Phytogeography differs greatly from zoogeography both in methods and results. Owing to our lack of knowledge concerning the modes of dispersal and the apparent want of certain species being restricted to definite modes of dispersal, the results of Historical Phytogeography are often to be obtained by statistical rather than by direct methods. Before really trustworthy conclusions may be expected, great numbers of species will have to be checked, relatives to their possible taxonomical and geographical history."



plants predominate. They are the individual organism, plant communities, biotic communities, vegetation, and ecosystems (Tansley 1935). The point of view is radically changed when one considers the geography and ecology of natural areas as established on a basis of plant communities (Thurmann 1849). No longer are the kinds of individual organisms the basic material dealt with, but the kinds of aggregations which they form.

It immediately becomes necessary to make certain distinctions, in addition to that already made between floristic and vegetational phytogeography. We must recognize the difference between the plant community in the concrete and the plant community as an abstraction or type. The former is a single, specific entity of aggregate character. It has limited spatial boundaries and a rather completely describable composition and structure. The latter is a conception of the community type which is based upon a knowledge of a series of separate individual community stands which are more or less similar. One is the association individual, the other is the association *per se*.

A third useful distinction is between the association and vegetation. In consideration of vegetation we are concerned with all the different types of communities in an area of any size. In a study of associations we make comparisons among similar association individuals or stands which are scattered as partial occupants of several areas. The European plant sociologists seem largely to be concerned with studies of associations; the British and American ecologists have more to do with vegetation, studying the several types of communities, both seral and climax, of a region. No American plant association, I believe, has yet been studied thoroughly and throughout its range in the manner of the plant sociologists, although there are some good localized studies of associations (Braun 1942). On the other hand, there are many studies of the vegetation of certain areas (Cooper 1913, Gentry 1942, Gleason 1910, Marie-Victorin 1935, Nichols 1913, 1918, Raup 1934, 1935, etc.) and some of extensive regions (Shantz and Zon 1923) or of the world (Rübel 1930).

The field which is coming to be known as bioecology has to do mainly with the study of biomes. Ecologists usually think of animals as one of the factor groups in the environment of plants, or as plants and plant communities as a part of the animal's environment. To the bio-ecologist (Carpenter 1941, Clements and Shelford 1931, Egler 1942, Phillips 1931, 1935) the biome is a super emergent whole or community composed jointly of plants and animals. Although such titles of studies as that of the "Grassland biome" (Carpenter 1940) make only a partial transition to the new view, that of the "Beech-Maple Red-backed Salamander Association" (Clements and Shelford 1939) goes the whole way.

In a discussion of vegetational phytogeography and the characteristics of natural areas it is necessary to note the school of ecological thought which pays

homage to the monoclimal hypothesis.<sup>2</sup> That the plant communities on the ground and the cover types that can be observed often bear little resemblance to the supposed ultimate climax, makes little difference to the believers in the monoclimal. Neither are they greatly concerned with soil differences for which no present knowledge warrants the assumption that reaction has the ability to overcome them (Davis and Richards 1933); nor with topographic features which are inimical to the climax and which can be changed only by the geological processes of base-leveling. For those ecologists, correctly, time is long; but whether one subscribes to the monoclimal hypothesis or to the polyclimax concept does make a great difference in the nature and extent of the natural areas which are recognized and mapped, and the terminology of communities which is employed.

There is no intention here to deny the processes of succession and the existence of comparatively stable climax communities which may result, but the purpose is rather to emphasize the difficulty if not impossibility of distinguishing between climatic climaxes (the adjective is redundant in Clements' system), and various other stable communities such as understood in Nichols' (1917, 1923) edaphic or physiographic climaxes, Godwin's deflected succession (1929), relics, and the like. The adherents of the monoclimal hypothesis assume that everywhere within the region of a general climate there is one type of climax vegetation and that all other communities are stages in the process of succession toward the climax. True the monoclimal ecologists recognize that in many instances some communities quite different from the climax may be as stable as the climax (the so-called subclimaxes and serclimaxes); but in some future millennium the habitats will not be so dry or so wet, so cold or so hot, and will attain the mesophytism which the climax requires. At this time the subclimax will advance to the climax. Clements himself pretty generally avoided the complications of detailed local studies and successional diagrams, but not so his followers. These numerous enthusiasts draw complicated diagrams which show every community of an area linked by succession to a single climax community. They very often have not understood Clements well enough, for his system, with the faciatiations and the lociations which it allows, provides for a variety of phases, or more or less local differences in the climax association—the faciatiations and lociations. In this sense the monoclimal is not at all a single ultimate community type, and Clements' monoclimal hypothesis is not much different from the polyclimax hypothesis of other ecologists. One is led to wonder to what extent the problem is really one of semantics and only an academic exercise.

The stable communities which are not true climax are explained on a basis of the modifying effects of (1) microclimate as related to topography, (2) soil

<sup>2</sup> The earlier Clementsian concept of the ultimate prevalence of a single climax plant formation, with its comparatively few mainly floristically distinguished associations, within the area of a single general climatic type, is merely extended in the concept of the biome.



types as related to the underlying rocks, topography, microclimate and vegetation, and (3) the history of the vegetation of the region, especially since the Pleistocene and the age of man's disturbances. In view of the fact that the true climax can develop only on the sites that are medium with respect to the total complex of environmental factors, and not where the sites are, in some characteristic, extreme; and in view of the fact that biotic reactions on the site can not change it sufficiently for the attainment of the climax, but only the geomorphological processes acting through geological time; it seems that the linking of all stable communities to the climax is highly hypothetical and serves no useful purpose. This is a point of view strongly developed by Domin (1923), and to which I subscribe.

The climax is said to be the "highest type" of vegetation that can be developed under a given climate; but what is the meaning of the adjective in this connection? Certainly more is meant than mere stature. Will this criterion stand analysis? Which, for example, is a higher type of vegetation, tall-grass prairie or its inclusions of "post-climax" oak woodland? The prairie prevails, but trees do well when soil conditions are suitable. Another constant expression in the characterization of the climax is that it is "best fitted" for the prevailing climate. How does one measure the fitness when a considerable variety of communities is stable?

Like Domin, I do not believe that the world's vegetation is tending toward a small number of climatic climax. Let us see what we have on the two sides of the ledger. The climax is the highest type of vegetation that can develop under the prevailing climatic type; it is the type best fitted for the climate; it is capable of self-perpetuation; it occurs only on the most favorable sites where neither the soils nor the microclimate are extreme for the area; it is potential on all sites, but its realization must often await geomorphological changes of a very slow nature. In confirmation of the climax hypothesis are the fact that successions are known; that soils do mature under the joint action of climate and vegetation; and that base-levelling does go forward. On the opposite side of the ledger, in addition to the difficulty of measuring fitness and what constitutes the highest type of vegetation, we can note that even on a peneplain there are site differences and corresponding vegetational differences. Furthermore, climate is a statistical summation of a large number of variations in time and over space. Actually, the so-called prevailing climate does not exist but is made up of a series of microclimates just as the association does not exist but is wholly composed of faciations and lociations. Living organisms must contend with, in fact can only contend with, microclimates; with local soil conditions; with the competition of their immediate neighbors, etc. On a basis of this line of reasoning, the climax is just one of a series of stable communities in harmony with local conditions, and is no more than any other so-called edaphic climax. It is merely the edaphic climax of non-extreme sites.

The monoclimate hypothesis, I believe, has been not so much an ecological touchstone as a millstone.

Finally, in this section of the essay, we should recall the antipodes of thought about the association. At one extreme, following the philosophical pattern laid down in holism and emergent evolution, Clements (1916, 1935, 1936), Phillips (1935), Morgan (1926), Smuts (1926), Wheeler (1928), and others refer to the association as an organism (sometimes as a quasi- or super-organism) while at the other extreme Gleason (1926) expresses a belief in the individualistic association. Some of the foregoing remarks are pertinent to this topic, and it will be returned to in later paragraphs.

#### RELATIONS BETWEEN FLORAL AND VEGETATIONAL AREAS

It seems generally agreed that plant associations must have a floristic characterization. Writing for the Paris International Botanical Congress, Flahault (1900) recalled that Humboldt introduced the term in 1801 and in 1807 gave primary importance to "associations végétales," showing their relations to various environmental factors. This idea was further applied by de Candolle (1820) who insisted on many details concerning the association such as its stations, local variations, the frequency and rarity of plants, groupment into societies, etc. Flahault said that some species of the association are dominant by the action which they exert on the habitat, and they characterize the vegetation of the country by their form, height, number of individuals, etc. Others are secondary or subordinate, and it is always the dominant species which characterize the association. In this sense the term "association" was similarly used by Warming in Denmark (*Plantesamfund*), Kerner in Austria (*Pflanzenverein*), A. Nilsson in Sweden (*Vaxtsmhälle*), Höck in Germany (*Bestand*), Schröter in Switzerland (*Genossenschaft*), Robert Smith in Scotland, etc.

For the Brussels Congress Flahault and Schröter (1910) said that it is now generally agreed that the association should be regarded as a grouping subordinate to a formation and of *definite floristic composition* (cf. Warming 1909). It follows from this, it seems to me, that in different geographical localities there will be different associations, even though the climatic and edaphic situations are very similar, because the component species must be drawn from different regional floras. These floristically different but ecologically similar associations are the "Formationsglieder" of Drude and the "varieties of associations" of Warming.

Flahault and Schröter repeat a paragraph written by Flahault in 1900 that is of sufficient interest to quote here: "The plant association is the final expression of the struggle for existence and of adaptation to the environment in the grouping of species. . . . The term plant association does not imply a harmonious concurrence of diverse activities working towards a common end, as in every society founded on division of labour. It is applied to the coexistence of forms, which specifically and morphologically are

foreign to one another, each having as its object its own exclusive profit. They live side by side according to the similarity or the diversity of their requirements, which find their satisfaction either in the same conditions of environment or in conditions determined by the presence of other organisms." The authors continue by stating that all species should be considered in the characterization of the association (although the name of the association may come from dominant, frequent or characteristic species, or even from the appearance of the association), and that no investigator has the right to prejudge the significance of certain species. The most numerous, the tallest, the most "peculiar" may not be the most important.

We come on down through the present century to the statement of a committee writing for British foresters and ecologists. Richards, Tansley, and Watt (1940) say that the vegetational object to be studied is a stand or example of an association that is characterized by its total flora. The particular stand may or may not be typical of an association, but the criterion is the presence of particular dominants and a particular flora. When different associations show agreement in the life form of their dominants, there is a similarity of essential habitat, especially of regional climate, and they belong to a larger collective unit which is called the formation, whether or not the component associations are partially or wholly different from a floristic point of view.

We have through all such writings the tacit assumption that the association is floristically characterized and has objective reality, although it is apparent that the geobotanists are somewhat bothered by the fact that the floristic assemblages of certain, often numerous, stands are not typical of any recognized plant association, nor simply transitional between two associations.

If we assume for the moment that an association does have objective reality, a question which will be returned to, and also accept the floristic characterization of an association, then it seems to me that it follows that *an association can exist only within the limits of a small homogeneous floristic territory where all stands have equal chances of containing all the same species*. Associations are then immediately seen to be very local phenomena. To just the extent that species areas are individualistic, so the associations must be individualistic in that they can be no more extensive than the territory of superposition of areas of the species which are involved.

This point can be illustrated by reference to the so-called northern hardwoods of foresters which are essentially the same as Clements' beech-maple climax association. In Central New England (Cline and Spurr 1942) this association is 82 per cent beech, hemlock, and sugar maple with the remainder composed of black birch, white ash, yellow birch, basswood, and a very small amount of red spruce. In comparison with a single stand of the beech-maple type in southwestern Michigan (Cain 1935), the New

England association is comparatively poor in tree species. The following Michigan members of the particular stand are either absent from the locality in southwestern New Hampshire or, if there, do not enter the climatic climax which is described by Cline and Spurr for low and mid-slopes; *Acer rubrum*, *Carya cordiformis*, *C. ovata*, *Celtis occidentalis*, *Liriodendron tulipifera*, *Prunus serotina*, *Quercus alba*, *Q. borealis maxima*, *Ulmus americana*, and *U. fulva*. Furthermore, the following members of the small tree layer are not reported for the New Hampshire climax association: *Amelanchier laevis*, *Asimina triloba*, *Carpinus caroliniana*, *Cornus florida*, and *Prunus americana*.

If we now drop down to the Southern Appalachians certain stands of trees occur there that are dominated by combinations of beech, sugar maple, hemlock, basswood, and yellow birch, which are the usual dominants or codominants of the beech-maple association. But what are their associates? Here we find peawood (*Halesia monticola*) very often codominant with sugar maple (Cain 1943) and *Liriodendron* codominant with *Tsuga*. *Aesculus octandra* and *Tilia neglecta* often codominant, and common associates of greater or lesser abundance include *Magnolia Fraseri*, *Magnolia acuminata*, *Ilex opaca*, *Cladrastis lutea*, *Oxydendrum aboreaum*, and *Quercus montana*. These are all absent from Michigan and New Hampshire beech-maple climax forests, just as *Betula papyrifera*, for example, is absent from the south. I am not referring to the mixed mesophytic association of the south, but, perhaps, to "Northern hardwood" segregates in the Great Smokies.

A critic of this point of view would say that I have here selected illustrations from three corners of the range of the Clementsian association characterized by beech-maple-basswood-hemlock-yellow birch, and that these are probably faciations of the associations. One can point out that if numerous examples were given of various stands of the association they would form a merging or continuously varying series with all possible combinations among the characteristic dominants. Furthermore, one could find all possible combinations of one or more of the dominants with the codominant condition, here and there, of a very large number of associates, and a still larger number of minor associates which never become codominant (Society of American Foresters 1932). To confound confusion, it should be noted also that each of the characteristic dominants of the beech-maple association occurs here and there as a codominant with the dominants of other associations, such as chestnut, white oak, shagbark hickory, etc., and even of other formations, such as red spruce or evergreen magnolia. The New England, Great Lakes, Southern Appalachian and other faciations must inevitably exist in an association conceived so broadly, because of the existence of floristic areas, of climatic gradations, and of differences in history.

Is it not better to reserve the term beech-maple association for a much more homogeneous type of vegetation than that designated by Clements, perhaps

to that portion lying north of the glacial boundary and definitely dominated by the two species indicated by the name? If such a suggestion is followed, one finds that there are numerous associations, rather than a few, and that even these are classificatory approximations made for practical reasons. Specifically, beech-maple association in this narrow sense is as impossible of exact delimitation as in the broader sense.

Professor Braun (1935a, 1935b, 1938, 1940, 1941, 1942, for earlier papers) is developing her historical explanation of the deciduous forest in this symposium, but a word in reference to it is useful here. She conceives of the mixed mesophytic forests of the Cumberland Mountains and vicinity as remnants or modern representations of the Tertiary mixed mesophytic forests. Out from this type, in which a large number of species hold varying degrees of codominance, are the association-segregates, which have been derived from the ecoclimax through environmental sorting of the species as conditions have changed. One of the large peripheral association-segregates (or perhaps a series of them) in the north and the east is the classical beech-maple forest north of the glacial boundary. But stands of beech-maple occur elsewhere, even within the general area of the mixed mesophytic forest, as local segregates on suitable sites.

Earlier than Miss Braun, Clements (1929) had recognized the significance of the historical developments expressed by the concept of association-segregates, as shown by the following quotation: "The faciation portrays the most recent differentiation of the association in response to climate, just as the associations of a formation represent the earlier climatic modifications of the latter. The faciation is the key to understanding the structure and response of all large associations and its recognition has become essential to further advance in the study of climatic communities and their phylogeny." Despite this, however, the old tripartite associational structure of the American deciduous forest is maintained in the second edition of the text (Weaver and Clements 1938).

I can not see that the association, as usually understood in either the large or the small sense, has objective reality. That which passes best as an association is a series of stands in a local area where there is an overlap of the areas of a series of species, and each species is equally available on the various sites. Within such an area of overlap of the ranges of those species which have approximately the same ecological requirements, the beech-maple aggregation, for example, will repeatedly occur in one of its faciations or locations, as will other aggregations on other sites. But on shifting geographic position a comparatively short distance in any direction new species will be added and former species dropped from the typical floristic composition of the new area. And the limits of such faciations, and even of the association itself, will be discernible only where there are natural floristic boundaries. Thus the phenomenon of the superpo-

sition of local areas of species from among those of a floristic territory results in association individuals and local association types. The association concept, with these limitations recognized, has considerable usefulness, but it is a strictly local phenomenon and even then not subject to severe definition.

We have seen that there is a very close relationship between small floristic territories and local plant associations. In fact, I believe that a series of stands which meets the definition of association can only develop within a single floristic area. This does not mean that there is no difference between floristic and vegetational phytogeography—there are differences in objectives, materials, and methods, but a suitable recognition of the very important role of floristic availability in community organization and the local nature of communities should help break down the sharp compartmentalization in geographic thought.

The data which have been presented are sufficient to make important the question of what is the climax association, to keep to our example, in which beech and maple play a dominant role. If a climax association is one in which a limited number of codominants plays a definite role in the composition of the type, there are numerous types in the American deciduous forest in which beech, for example, plays a role. If, however, one or more of the codominants may be missing or of minor importance in some stands of the association without doing violence to the concept of the association type, then the association looks to me to be a very tenuous and poorly delimited concept. Between these two possibilities ecologists and plant geographers are faced with a dilemma of practical as well as theoretical significance.

The question that has been raised can be underlined by one more illustration. Professor Aaron J. Sharp, who has recently returned from two years' field work in Mexico and Guatemala, reports beech forests in the state of Hidalgo. The beech is called *Fagus mexicana*, but it is nearly if not identical with the beech of the higher southern Appalachians.<sup>3</sup> The Mexican beech forests, in which trees may exceed 30 m. height and 1 m. diameter, occur at Tutotepec and Zaualtipán, usually on volcanic soils, north-facing slopes, and at altitudes around 5,600-6,200 ft. At Zaualtipán *Epifagus virginiana* is parasitic on beech roots as it is in the United States and there and at Tutotepec a common codominant is *Magnolia Schiediana*, which is a close relative of *M. grandiflora* of our southeastern states. *Liquidambar styraciflua* is also a common associate of the beech both in Mexico and the Southern Appalachians.

Other species giving the beech woods of Mexico a northern cast belong to such genera as *Cornus*, *Prunus*, *Quercus*, *Pinus*, *Carpinus*, *Ostrya*, *Alnus*, *Salix*, *Rubus*, *Styrax*, etc., and *Gelsemium sempervirens* and *Ascyrum hypericoides* occur as they do in the States. But in strong contrast to these Holarctic forms are the tree ferns of the genus *Cyathea* which

<sup>3</sup> In a personal communication W. H. Camp, who is studying the beeches of the Northern Hemisphere, informs me that this beech extends northward along the crest of the Appalachians, approaching sea level in Nova Scotia.

are frequent in the undergrowth, arborescent species of *Gaultheria* and *Vaccinium*, *Citharexylum* Pringlei, and members of *Laurus*, *Eugenia* Befaria, *Fuchsia*, and *Ardisia*.

At the risk of laboring my point and belaboring my audience, I want to add one more illustration of the indefiniteness of the association or community type. A few years ago the Estonian, Lippmaa, who became well known for his concept of the unistratal association (Lippmaa 1934, 1935, Cain 1936, Gleason 1936), published a paper on the Galeobdolon-Asperula-Arisaema Union (Lippmaa 1938). This union or unistratal association is the herbaceous layer society composed of geophytes and hemieryptophytes that everywhere accompanies (or is an integral part of) the temperate, broad-leaf, summer-green forest. Lippmaa (1938, Cain 1943) showed that these herbs in the main must have been associates also of the Aretotertiary undifferentiated broad-leaf forest; but the feature of this study which is of most interest for the present discussion is the following. He approached his problem and the characteristics of the herbaceous layer community from the point of view of a botanist of the Baltic area. Consequently the typical composition and structure of the union was taken to be that of his area, and varieties of the union were described for Asia, for the Balkans, for southern and western Europe, and even for North America. By presenting maps of the areas of the species of the community as it occurs in the Baltic area he graphically showed a feathering-out of the constant and characteristic species as one studied the layer community at stations which are farther and farther removed, while at the same time new members of the community make their appearance.

It is quite evident that had an American or Chinese, or even another European ecologist gotten the same idea as Lippmaa and launched upon the same kind of study starting with the floristic composition of the union in his home territory, he would have considered the Baltic communities as forming a variant of the association which occurs in typical form in his own backyard. And had the student in eastern Asia, or some other place, prepared maps of the areas of the characteristic and constant species of the layer community as he knew it, he also would have found a feathering-out of the species with distance, and the addition of new ones not found in his area. Finding the floristic composition different in and around Estonia, he would have written of the Baltic Galeobdolon-Asperula variant of the union.

What I am spot-lighting for your attention is not the provincialism of the geobotanists, but the provincialism of the floristic composition of communities.

#### DOES THE ASSOCIATION HAVE OBJECTIVE REALITY?

To the vast majority of geobotanists (ecologists, geographers, sociologists), bringing into question the objective reality of the plant association must seem heretical, today as it did to Nichols (1929) when he criticized Gleason's essay of twenty years ago on the individualistic association. For them it is the *sine*

*qua non* of their science. The association is compared to the species. Just as a species is made up of the individuals of a kind, so is the association made up of association individuals. Just as the species description is a synthesis of the characteristics of the individuals of the kind, and can be typified by a selected individual, so the association in the abstract is a synthetic concept and can be typified by a stand or group of stands. However, believing that associations and species are not phenomena with the same objective reality, I wish to add my voice to the few, among them Gleason (1926, 1936), del Villar (1929), and Gaussen (1933), who have objected.

The drawing of a parallel between associations and species is not tenable. The members of a species are related by decent and reproduce their kind; the members of an association have no such genetic connection. They arrive at their more or less similar state by the successional route from a variety of beginnings, and reproduce their kind only by the most devious and protracted labors. The individuals of the most variable species have nothing like the motley array of antecedents that bring forth the associations. In the work of the phytosociologists there is a grouping of associations into alliances and orders in a manner similar to the grouping of species into genera, families, etc., but if the basic unit lacks objective reality, the hierarchy must be even less sound.

The phytosociologists who have the strongest faith in the integrity of the association believe that the floristic assemblage is the primary feature of the association, and that the association can be studied in terms of its constant species or its characteristic species just as the species can be studied morphologically without preoccupation with its biology or ecology. For the Scandinavian phytosociologists the association is characterized by the constant species, a certain number of species for any association which reoccur in every quadrat and every stand examined with a regularity of 80 to 90 per cent, and usually with a considerable dominance or coverage. These are highly social or gregarious species. For the members of what we may call the Braun-Blanquet school of plant sociology, which includes most of the phytosociologists from Holland to Italy and from France to Poland and the Balkans, the association is recognized by its characteristic species which have a high degree of fidelity to the floristic assemblage which is called the association. These may also be called indicator species.

These investigators only secondarily concern themselves with questions of life form and the physiognomy of the plant communities, and with the relations of the communities to the habitat. Their approach is in the first place a floristic one. Let us examine further whether the association is definable in these terms.

There are certain facts in nature which the plant geographer can study. The species are facts, in most instances at least; and the areas of the species are facts which can be considered with reasonable preciseness. Environments are facts. There are recogniz-



able habitats. They can be rather well described for small enough areas; but we are confronted with merging phenomena and larger areas are progressively more poorly delimitable. The life form of a species is a fact, and the physiognomy of an aggregation of species is describable within acceptable limits. But does the association in the abstract, characterized by its floristic assemblage and the special features of certain of its members have a comparable objective reality? I do not bring into question the reality of the stand, which is the concrete example of an association (the *synécie* of Gaussen, the association individual of Braun-Blanquet, the fragment of association of DuRoi), but the reality of the abstraction—the association as a composite of the several association individuals.

In nature there is a habitat. It is occupied by plants of a number of species. The number of species composing the community of the habitat and just which ones they are depend upon several factors: the available flora, the ecological characteristics of the species that are available, the chances of and the time which has been available for dissemination into the area of the habitat, the competition among the members, and their life forms. The individual plant community has objective reality—sharply delimited at its borders if the habitat changes strongly in a short space, poorly delimited if the habitat changes gradually over a greater space. But so far as the flora of the community is concerned, it is the result of the superposition of areas of the species. Each species of the stand will have its individual and often quite different total area, and each has a more or less different ecological amplitude and modality. They live together in the particular community because they chance to have overlapping areas and are biologically successful in the particular habitat.

When comparing different stands that are similar, unless one blindfolds himself by preconceptions of the reality of the association in the abstract, it is soon realized that the farther removed one stand is from another the more different are their floristic assemblages, as Gleason emphasized in his paper on the individualistic association. Here arise the questions which have always plagued the phytogeographers: how different can two association individuals be and still belong to the same association? What is to be required in the way of constant or characteristic species?

The investigations of the phytosociologists produce results with the appearance of a high degree of accuracy, with statistical data on coverage, frequency, density, constancy, and fidelity, in impressive tabular comparisons of stands of an association. And yet it seems to me, having tried these methods myself, and without impugning the honesty of the investigators, that there is more artifice here than science in the selection of stands for representation of the association. Let us examine a little more closely the concepts of the association which have so far been mentioned.

In the north, especially in the general regions of

taiga and tundra, where the flora is not rich in species and where under rather rigorous climates edaphic conditions are frequently abruptly changing and more or less submarginal, the concept of the association as defined by constant-dominants is claimed by the Scandinavians to work fairly well. This is, I believe, merely a matter of degree, and northern community types have in the last analysis no more reality than those of lower latitudes, but there is often a close coincidence between associations so defined and community physiognomy and habitat. In the south of Europe, however, the concept has already lost much of its usefulness and the Braun-Blanquet school emphasizes fidelity. And in the tropics the association often can not be defined in terms of either constant-dominants or species of high fidelity. In any part of the globe, however, when the habitat is in some manner extreme and the adapted species comparatively few in number, simple communities with constant dominants and characteristic species occur. But no worldwide treatment of vegetation seems possible on a basis of these concepts, and the acceptable definition of an association has to be different for different regions and different purposes.

The weakness of defining associations on a basis of the so-called characteristic species of high fidelity to an association is well illustrated by an example pointed out by Gaussen (1933). For the association *PICEETUM EXCELSAE* Braun-Blanquet gives as characteristic species *Listera cordata*, *Pirola uniflora*, and *Lycopodium annotinum*. An examination of the total areas of the *Picea* and these three characteristic species of the association shows that they are by no means the same. Furthermore, *Listera cordata* is associated with *Pinus uncinata* in the Pyrenées, *Pseudotsuga mucronata* in Vancouver, *Abies balsamea* and *Pinus strobus* generally in northeastern America, as well as with peat bogs. *Pirola uniflora* is associated with *Picea alba* in Alaska, and *Picea Engelmanni* and *Pinus aristata* in Arizona. *Lycopodium annotinum* is associated with *Pinus strobus* in New Brunswick, *Tsuga canadensis* in the Appalachians, and *Picea sitchensis* in the Pacific Northwest. As Gaussen says, these species do not have any direct bond with *Picea excelsa*. They are as characteristic of other associations as of *PICEETUM EXCELSAE*. To believe that they define the *Picea excelsa* association, except possibly in a comparatively small area, seems illusory. The various conifers probably have some importance for these species of the undergrowth, but it is unlikely that the presence of these herbs makes any difference for the conifers. The occurrence of *Pirola* and *Listera* is probably limited in part by the occurrence in coniferous litter of suitable species of mycorrhizal fungi.

We have been dealing with three sets of phenomena: (1) floras, the areas of species, and floristic assemblages which result from the coincidence of areas; (2) habitats or various complexes of the factors of the total environment; and (3) the life forms of species and the physiognomy of vegetation. Of these it would seem that physiognomy takes a pre-



eminent place for the broader aspects of plant geography, with the floristic assemblages and the characteristics of the habitat of more local importance for the lesser communities. Analyses of habitats and the description of environmental complexes, in so far as they are possible (and there are drastic limitations) cannot take first place in the recognition and definition of plant communities. The plant life itself must be first. It likewise seems apparent that the floristic assemblage of communities is secondary to physiognomy for plant geography, for the former is a local phenomenon and the latter a much broader one. If we compare, for example, the summergreen forests of America, Europe and Asia, or even the beechwood types of this forest, we find that the environment has imposed a certain characteristic physiognomy and only permits certain floristic assemblages which are more or less different in each area.

The idea of the association in the abstract, comparable to a species, has no validity and is by no means of any universal applicability to vegetation. The association as a concrete individual stand does have objective reality. Such communities can be mapped. Their physiognomy can be studied, their constituent flora listed, the habitat described, the social and dominant species examined, and the dynamics of succession dealt with. The prodigious labors involved in quadrating and the statistical comparison of stands can have little more than local significance and are certainly not the pivot of geobotanical techniques.

Having denied that the association has objective reality, and developed a sort of twentieth anniversary affirmation of Gleason's individualistic association hypothesis, I do not wish to deny that it is sometimes useful in ecology to pigeon-hole stands in approximate type groups. But it must always be remembered that community types or associations are metaphysical approximations in a field where there are unlimited variables, combinations and permutations. Between the individual stands at one end of the scale and the largest world formation types at the other (such as the broad-leaf summergreen forest), there can be few if any precise sub-divisions. Although the Society of American Foresters recognizes nearly a hundred forest types for eastern North America, every student of the problem finds in his particular region many stands that do not fit well with any of the described types and are not merely ecotonal combinations between types. As the deciduous forest types merge into one another, so the summergreen forest as a whole merges with the taiga, the subtropical evergreen forest, and the grassland.

Certain conclusions have been stated or implied at various points in this essay. Some of them and some of the points of view expressed will not meet with total agreement. We very seriously need more field investigations and less theorizing about vegetation.<sup>4</sup> For example, we have some good local objective studies of vegetation, but we do not have adequate extensive field studies of associations. With-

out such studies debate concerning the individualistic nature of the association (See Nichols, 1929, criticism of Gleason) can produce some heat but not much light.

#### CONCLUDING STATEMENT

My general conclusion is that plant geographers have a largely unfinished task in the adequate study and description of existing vegetation, and that much of their work must be in terms of natural areas. In this connection I am wholly in agreement with Edward H. Graham (1944), who says that the term "natural area" is a very useful and realistic one although incapable of exact definition. One virtue of the term is its very indefiniteness. Like the general term "community," it does not commit one to the necessity of certain difficult decisions; but it is an even broader term than community, suggesting a recognition of the simultaneous action of all operative factors and the joint existence of such diverse phenomena as organisms and different physical states of the atmosphere, soil, etc. A natural area, then, is a geographic unit of any order of size with sufficient common characteristics of various sorts to be of some practical usefulness in biogeography. Wildlife managers, grazing and forest administrators, and other working ecologists approach such a usage in their common practice.

It does not follow from this argument that students should discontinue their efforts toward analytic studies of the environment, the fauna and flora, and the communities, nor that efforts toward synthesis and classification are to be abandoned. It is suggested, however, that it be kept in mind that single-factor operation does not occur in biological nature, that the environment apparently can not be completely analyzed, and that diverse analytic data can not at present be synthesized back again into anything like the natural whole of the ecosystem. Elsewhere I have called this the "Humpty-Dumpty problem," and "All the King's horses and all the King's men can't put Humpty-Dumpty back together again." When all these limitations of phytogeographical study are kept in mind, one finds that many useful approximations can be made, coincidences observed between biological phenomena and physical ones, and classifications erected. The temptation of standardization and the erection of supposedly universal systems is more easily avoided and natural objects are not cut or stretched to fit the bed of Procrustes.

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<sup>4</sup> Such as this paper.

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EVOLUTION OF CERTAIN FLORISTIC ASSOCIATIONS  
IN WESTERN NORTH AMERICA

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IN A SYMPOSIUM ON  
ORIGIN AND DEVELOPMENT OF NATURAL FLORISTIC AREAS  
WITH SPECIAL REFERENCE TO NORTH AMERICA

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## EVOLUTION OF CERTAIN FLORISTIC ASSOCIATIONS IN WESTERN NORTH AMERICA

### INTRODUCTION—CONCEPT OF FLORISTIC EVOLUTION

In discussing the evolution of a flora I assume that the events in the history of the flora have been such that its composition from one period to another has undergone developmental change. Never in successive geological times does the flora precisely repeat itself. By reason of the fact that both migration and persistence of plants can normally take place only as a result of reproductive processes, and because these processes almost inevitably set in motion the mechanics of population genetics, the nature of the population from time to time becomes, at least in part, a product of the variation in chromosome constitution, and variation in the amount of genic materials present among the individuals of the population. The population thus becomes subject to all of the phenomena of speciation that may result from any of various genetic processes as these may be influenced by the environment. Thus from a floristic point of view, genetic change, however great or small, is important, because it involves the development of the species population, and if persisted in, may lead ultimately to significant floristic differences. These genetic changes are, no doubt, one aspect of organic evolution. In their effect on the population and on the flora they also present one aspect of floristic evolution.

Not all aspects of floristic evolution, however, are of necessity linked immediately with genetics. To be sure, every species is the result of evolutionary processes but this evolution need not have taken place wholly within the history of the flora with which the species ultimately finds itself associated. Species may come into the flora from outside through migration and infiltration, and species may vacate the flora through extermination. It would appear then that migration and extermination are likewise important methods of floristic evolution and that they may function through time to keep the flora in a constant state of change. They operate through physiological activity within the scope of the theory of tolerance and the principle of limiting factors.

Plant migration must be construed as a movement of an interbreeding population and not as a movement of individuals, or as a movement of floras. It is accomplished in most plants chiefly through reproductive processes that usually set in motion the genetic forces that are essential to its success in traversing diverse habitat conditions and in meeting fluctuations of the environment. Environmental diversity must be met and overcome through the development of races of the species population whose tolerance spans are sufficiently diverse to enable the

population to cross by inhabiting such areas. The greater the genetic diversity of a population the greater are its chances of survival in the face of the hazards of migration. Variation in tolerance ranges and variation in genetic diversity among the species of such a flora would insure a very diverse response to any stimulus that might initiate the migration as well as to the diverse environmental conditions that would be encountered during the course of such a migration. Some species of the flora would inevitably perish in the migration and their places would be taken by new types better adapted to the conditions that prevail. Migration is therefore usually contemporaneous with the development of the population either through the building up or wearing down of its genetic pattern. In any event through such processes as organic evolution, migration, and extermination there are produced significant and continuous vegetational changes.

We may therefore conclude that floristic evolution is activated by the interplay between environmental condition and genetic and physiological phenomena that induce migration, bring about extinction, and select those genetic races within the species population that are preadapted to the new conditions. The production and selection of the genetic races must be construed as steps in the evolutionary process known as natural selection.

### CONCEPT OF THE PLANT COMMUNITY AND SIGNIFICANCE OF PATTERN OF AREA

We have discussed the role of interbreeding populations and of migration as these are involved in floristic evolution. The composition of the plant community or of the flora, however, reaches beyond the structure of any population of interbreeding individuals. It is usually made up of many such populations that show no close genetic relationship to one another. Each population of interbreeding individuals is within itself a dynamic system that carries on the functions of the population. These functions serve only the specific population in which they originate and not the community as a whole. Among these functions are the transmission of life, migration, and the maintenance of the population in adjustment with environmental fluctuation. The organic functions of the population, then, are solely the functions of population genetics and result from reproductive and genetic activity within the population. The functions of the individual, however, are physiological and lie wholly within the scope of the individual organism. Both of these types of function result from organic activity. Furthermore, there are no organic functions that operate between genetically

unrelated populations except in special cases such as are involved in parasitism and symbiosis. A community made up of such populations has neither organic nor functional unity but is an aggregation of independently operating populations of interbreeding individuals. Each such population functions strictly in its own behalf without consideration of any unrelated associated population.

We can agree with Gleason (1926, p. 26) as to the coincidental nature of the plant community but we should carry that idea further. The association owes its existence as such to the coincidence or overlapping of the tolerances of the component species and to the coincidental aggregation of its genetic lineages which have resulted from historical events. The individuals of two or more species can occur together only to the degree that the tolerance ranges for those functions that make simultaneous and similar demands upon the over-all climatic and edaphic environment actually coincide. Within this situation the make-up of the community will depend in certain cases upon the local occurrence of specialized conditions of the micro-climatic or edaphic environment to which some of the species may be adapted and for which there is no competition; and in other cases upon competition between individuals of like and unlike species that may make parallel demands upon the local environment.

The biotic factor with the possible exception of certain host-parasite relations and certain symbiotic relations, can be effective only indirectly through some influence of a physical nature. An organism may operate to alter a physical condition in the environment that will enable another organism to enter. The reaction of the new organism will be to the altered physical condition and not to the organism that produces the altered condition.

There are, however, certain relationships between a parasite and its host and between certain symbionts that would make their occurrence within a given community either wholly or partially interdependent. Sometimes this relationship is between a plant and an animal as between the yucca and the yucca moth. These cases, however, constitute relationship strictly within a limited and often mutual sphere and do not constitute relationship across the community as a whole. They, therefore, constitute the particular problems of special cases and many such interdependencies may exist in a community that bear no more than coincidental relationship to one another floristically.

The plant community then, possesses only coincidental unity based upon like simultaneous environmental tolerances for the over-all environmental factors. Hereafter in this paper in referring to this concept, I shall use the term "coincidence of tolerance."

In a previous paper (1946) I pointed out that the functioning of all plants, in their precise physiological reactions, is controlled by the conditions of environmental factors within the scope of the operation of theory of tolerance and the principle of limiting factors. Environmental conditions, with few

minor exceptions, occupy area independently of the occurrence of any species of plants that may depend on them. The over-all environmental condition, of necessity, had to develop independently of any flora that may have come to occupy the area. Because the plant population is adapted through genetic processes to a given set of environmental conditions, the presence of these environmental conditions determines the area occupied by such a population. The pattern of area, therefore, reflects only the condition of the environment to which the species populations inhabiting it are adapted. The pattern of area has no historical significance whatsoever that applies to the immediate flora as such. Historical facts pertaining to the flora must, of necessity, be established independently of the present pattern of area occupied by the flora. The historical events that brought to the area a pre-adapted population are coincidental and bear no cause- and effect-relationship that is significant to area and the development of the environmental condition that prevails. Thus the pattern of area, whether it be referred to as a "natural area" a "progressive equiformal area" (Hultén 1937) or any other concept of area that endows it with historical significance in relation to its species population, must first be thought of in terms of environmental conditions prevailing today to explain the flora that may exist upon it.

#### NATURE OF FLORISTIC HISTORY

Because of the differences in genetic constitution and in physiological capacity between the various species of the community, and because of the operation of different genetic mechanisms it is hardly to be expected that any two or more species of such a community will follow precisely the same historical pattern even for a relatively short time. The inevitable result is that even the coincidental unity of any particular assemblage of plants may be of short duration. It therefore becomes necessary, in tracing floristic records through time, to re-define the flora repeatedly in terms of the changed associates of some of the more persistent characteristics. Thus the redwood flora may be repeatedly redefined in terms of the changed associates of the fossil species, *Sequoia Langsdorffii*, a point to be discussed later. This is essentially the method used where migrating floras serve as horizon markers in geological time. Changed floristic composition as well as changed geographic position become the indicators of time.

Floristic history, because of the lack of reality of precise associations through time and because of the lack of functional unity of the plant community, becomes the history of an aggregation of independently operating dynamic systems, each of which is meeting its problems in its own way. Each species develops genetically and migrates, in accordance with the reactions of its individual members to environmental conditions. These reactions are influenced by the genetic diversity of the population and the range of variation of its tolerance spans. The species may expand or contract its total area. It may develop into

a number of genetic races each in turn capable of carrying the divergence further, or through adverse conditions its population may be reduced and ultimately exterminated. Each entity of the flora has had an evolutionary history that has involved genetic processes. It is important to realize that the genetic source of each entity must have been in the floristic association immediately preceding in the migration stream or in some contiguous association from which it migrated into the new association. The interlacing of these divaricate genetic lines becomes the pattern and the framework of floristic history.

From the nature of these dynamics it would be impossible to conclude that such a flora as the redwood forest has migrated as a whole from the north where it may have originated, because the redwood forest in its various elements originated at different times and at many points over the area it traversed and some of its elements developed in association with other floras from whence they migrated into association with the redwood flora. It is important to point out, in this connection, that at all times the available land area of the earth was totally covered by vegetation. In other words, on any land area, vegetation is continuous in time and space. It is difficult, under these conditions, and in terms of such dynamics as herein outlined, to envisage such floristics as an Arcto-Tertiary flora (Chaney 1936) in contrast to a Madro-Tertiary flora (Axelrod, *Mss.*) as accounting for floristic sources and centers of origin during Tertiary time. Such concepts of floristic organization and development demand unity and stability of communities in time and space beyond what is possible in the light of the nature of floristic dynamics such as are bound up with the genetics of the population, the physiology of the individual and the diversity and fluctuation of the environment. They are often thought of as demanding centers of origin from whence floristically organized migration streams radiated. Origins must be construed as being potentially possible over this whole land area at all times. They must be further construed as involving the particular problems of special cases in each of the many genetic lineages as these may be influenced by environmental and genetic phenomena. They must not be construed as involving unit floras or unit floristic elements and components. The apparent unit flora or unit floristic element in floristic history is a coincidental aggregation whose interpretation is fraught with the hazards of the incompleteness of the palaeontological record, and with the difficulties of identification from fragmentary materials as these are concerned in the piecing together of phylogenetical lineages. This does not mean that migrations have not taken place and that many species have not been concerned in more or less parallel migrational histories of varying duration. It does, however, open to question the concept that these parallel migrations are in any sense more than coincidentally floristic or that they represent floristically anything more than very unequal associations of species or genetic lineages through time.

We may conclude that any flora has had a complicated evolutionary history whose interpretation must be sought by piecing together genetic lineages. We may begin in each separate lineage with the distributional pattern of vicarious species as they occur today and seek aid from the fragmentary history left to us in the fossil record. We must lean heavily upon the logic of phylogenetic and physiological interpretations. So divaricate and interwoven are the patterns of associational relationships of these lineages that it is doubtful if it is now possible to assign any lineage as a whole to any definite associational relationship having historical significance as to point of origin or centers of dispersal, except in cases where the lineage has remained simple for a long time, or where its inception has been in the later geological periods or has remained within very narrow physiological limits. Even then the association and its continuity must be interpreted in terms of the limitations imposed by its coincidental nature. The best evidence of closeness of recency of relationship between two floras rests in the largeness of numbers of vicarious species or other smaller taxonomic categories. This evidence is further strengthened, although not absolutely so, when the physiological requirements of such paired entities are also close. Rarely is the fossil record adequate to depict the framework of the story. It is too localized and infrequent in time and space and too limited as to its ecological representation of the flora as a whole. It must therefore serve chiefly in a corroborative capacity to support ideas drawn from other sources and to embellish the story locally with details. It, however, is the only source of real fact and hence is most important.

As yet we have little or no evidence as to the limitations of species through time. From what we now know genetic lineages may be divaricate as well as reticulate. The unit-taxonomic interpretation of the lineage through time will be plagued by continuity. It is only where the story is broken or where we may get "momentary" glimpses of it as we do in the fossil record, that it will appear to be broken into species.

#### SOME POINTS CONCERNING ENVIRONMENTAL CONTINUITY AND CHANGE

When we consider the spheroid shape of the earth and the nature of insolation it seems evident that even on an ideally smooth globe there would always be a climatic gradient from the equator to the poles that in its simplest state would result from variation in the angle of incidence of the sun's rays and the variation in thickness of the atmosphere that these rays would have to penetrate before reaching the earth. It is possible, at some times in the past, that the magnitude of the gradient with respect to certain features of climate might have been less than at other times but on a globe a gradient of some magnitude is inevitable. Add to this situation a rotating earth with surface features of varied relief and varied land and water areas and the gradient will

exhibit a very complicated pattern which has undergone considerable local fluctuation through time. Such a situation will tend to perpetuate a diversification of the floristic setting from equator to poles. The diversification will be intensified in regions of greater aridity or during arid periods and conversely will be more homogeneous under conditions of greater humidity. This results from the operation of the law of the minimum (Liebig 1843). As one approaches the minimum (in this case of the moisture factor) the greater will be the effect of differences of small amount.

Floristic history would follow these changes because of the selective capacity of the new environments operating on the products of the genetic diversity of the species population. Types with extended tolerances would be permitted to survive and either initiate new lines of development or, through back-crossing, serve to restimulate the pattern of genetic diversity of the population as a whole.

#### ON NORTHERN ORIGINS AND PERMANENCE OF CONTINENTS AND OCEAN BASINS

Since our thesis concerns floras of western North America that have left in the fossil record a considerable story of their migration and development, whose interpretation in the literature is replete with references to origins in high northern latitudes, it is important that we point to some of the problems inherent in such concepts as they relate to the stability of the earth. An earth, tilted on its axis relative to the plane of its orbit will inevitably be characterized by a darkened polar area that will alternate seasonally with a lighted condition. The duration of the darkness will vary to some extent with position but will range from a few days of total darkness to almost six months of total darkness. By total darkness I mean the absence of insolation capable of being converted into heat energy and of light of sufficient value for use in photosynthesis. The area so involved will be a disc approximately 3,000 miles in diameter. Receiving no insolation, such an area would soon dissipate any residual heat in its soil and rock surfaces. There would result extended and bitter arctic cold throughout the darkened area that would affect winter temperatures for considerable distances into subarctic areas.

If we assume now that the poles have been stationary as most astronomers insist that they have, and if we assume that the continents and ocean basins have been perpetuated in their present places through geological time as many geologists insist that they have, we must conclude that no tropical, warm temperate, or even temperate forest flora, could possibly live and develop in high arctic latitudes. It would be too cold on the one hand and too dark on the other hand. To raise the temperature in such an area and not change the long periods of darkness would only aggravate the situation because the increased temperatures would increase the respiration rate to the point that in evergreen species the reserve food supply would soon be depleted and deciduous species

would be forced out of dormancy before adequate light returned and they too would dissipate their food reserves through rapid respiration.

The occurrence of warm temperate floras such as the redwood forest in the fossil record of such high latitudes as Banks Land, Wrangel Island, Arctic Alaska and Canada, St. Lawrence Island and the subarctic Bering Sea region should serve as food for considerable thought on these problems. It should cause any informed biologist to view with suspicion any dogmatic statement aimed to categorically refute polar migrations and continental drift unless this biological paradox can be satisfactorily solved with the refutation. This is a controversy that calls for an open mind. It is a controversy in which facts are few and theory is rampant. The botanist can present as fact the occurrence of these fossil floras in what today are high latitudes. He can only point to the relation of environmental conditions to physiological and genetic processes as he knows them in the plants that exist today, in order to substantiate any argument he may wish to raise in behalf of his ideas. The problem, nevertheless, is one that every plant geographer must weigh carefully because it marks the parting of the way to very diverse conclusions. Thus far we can only conclude that if forest floras of the past actually lived and developed under such conditions in the high latitudes of the north, they could only have done so under permission of very different physiological relations than prevail in plants associated in similar floras today. To an informed biologist such a conclusion seems preposterous. To him it may seem that the same dynamics inherent in faulting, folding, overthrusting and in the maintenance of isostatic balances present a far more plausible mechanism toward the solution of these problems than does the "conjuring up" of complicated physiological mechanisms such as are unknown in any of the divisions of the plant kingdom today and are scarcely to be expected to have been involved in the physiological variations in the evolutionary span of any modern genus or species. Redwood forests just do not live in cold, dark, high polar latitudes; proof is needed that they ever did.

#### ON THE CONCEPT OF THE REDWOOD FOREST FLORA TODAY AND THROUGH TIME

Having outlined the framework upon which our argument is to rest we may now turn to some of the problems of floristic evolution that have been concerned in the history of vegetation in western North America. Chaney (1936) has pointed to the complicated migrational histories that have involved the Tertiary floras of North America. The particular migration stream that is most completely represented in the fossil record and has received greatest attention in the literature is that pertaining to the redwood forest. Its migrational history is incontestable, the fossils having been found in progressively younger rocks as one moves southward on the continent. Today the redwood forest is confined to the coastal



mountains of northern California and extreme southwestern Oregon.

We must inquire at the outset into the concept of the redwood forest as it exists today and as it has developed through time. When the species population associated with the coast redwoods is plotted on a map it is revealed that not a single associated species approximates a complete coincidence of geographic area with that occupied by the redwood. Most of the associated species overlap into the redwood area and extend widely beyond. Some extend northwest into British Columbia and Alaska, some to the Rocky Mountains and thence south into Mexico and some south along the coast to Lower California. Other species reach only to the Sierra Nevada or to the inner north coast ranges of California and into the southern Cascade ranges. Only a very few are confined to smaller areas circumscribed by the boundaries of the redwood. Here is a forest whose unity of concept is based upon the total range of a single species, *Sequoia sempervirens*, together with those associated species whose geographic ranges chance to overlap into its area. Here is a flora possessing coincidental reality resulting from the coincidence or overlapping of the tolerance ranges of the component species. It has reality only by virtue of its definition in terms of the occurrence of *Sequoia sempervirens* and when so defined it can be discussed as a unit with complete clarity of meaning. Because the redwood functions in accordance with the principle of limiting factors and the theory of tolerance (Mason 1936) it is also possible, at least theoretically, to outline the range of environmental conditions under which this varying association of plants occurs. This, I think, is the extent of the reality of the redwood flora, and possibly also the extent of the significance of its reality or unity.

We have, in this association, many species, each of which culminates continuous and divaricately branched genetic and evolutionary lines; some of these lineages may have run parallel for long times, while others may have undergone exceedingly complicated development and ramification resulting in offshoots that may have developed independently, or may have become exterminated, or may have merged again with other lines from the same original source. New and different lines may have migrated into the flora. The genetic changes resulting in the branching of these lines often involved changes in tolerance so that the progeny were able to tolerate different conditions and hence occupy a different area from that of the parents. One of these evolutionary lines has involved the redwood itself and shows little evidence of change through Tertiary time. Other lines have involved the various types of firs and the successive species that have resulted. We have still other lines representing the several groups of pines, the spruces, and the many other genetic successions of plants that have had a part in this history. In some of these lines evolution has been diverse, in others there has been little change; in some it has been rapid, in still others it has been slow. In any

event the history of the modern redwood forest is the sum total of the independent histories of the separate and interlacing evolutionary lines which have developed through diverse genetic processes and which have come from diverse sources. At any given time these plants were brought into association through the events of history by reason of and to the extent of the coincidence of their tolerances. However, through time a precise association has never repeated itself. There are floristic bases for distinguishing an Eocene redwood forest from an Oligocene redwood forest and a Miocene redwood forest from a Pliocene redwood forest. These floristic differences resulted from genetic changes, from infiltration from outside and from extermination. It is therefore necessary to redefine this association repeatedly in terms of the changed associates of the one persistent common denominator, the fossil species, *Sequoia Langsdorffii*. Although there is no continuity of the precise association through time, one cannot on the same evidence deny the thread of reality in any of the associated historic lineages.

Many of these genetic lineages may be traced through much of Tertiary time in association with *Sequoia*, however some have had their inception in different floristic histories and have migrated into association with the redwood at various times in its history and at various point in its migration stream. Mason (1934) has pointed to the history of *Vaccinium ovatum* as an associate of the redwood that entered the redwood forest probably in post Tertiary time. Some lineages have apparently arrived in the redwood association from a southern source and through evolutionary changes a descendant type took up a southward migration with the redwood. For example, *Umbellularia californica* may belong to a genetic lineage that originally came into the redwood forest from the south. *Umbellularia californica*, however, as a species in the taxonomic system, probably had its origin in the lineage after it reached the redwood forest and apparently developed in the north and migrated southward with the redwood. Thus the history of *Umbellularia californica*, as we know it in the fossil record, would give little evidence of the southern origin of its genetic lineage. One must use an approach to paleobotany that is taxonomic as well as floristic and lean heavily upon phylogenetic interpretation in order to work out the genetic lineages involved. Floristics in such studies are important as a rough guide to environmental conditions and an interpretation of physiological variation.

#### RELATION OF MODERN FOREST FLORAS TO THE TERTIARY REDWOOD

The genetic or evolutionary lines associated in the history of the redwood forest of the past are represented today by a geographic and taxonomic pattern of distribution of species over the whole area of western North America. Some of them no longer have representatives in the redwood flora. Some of them have representatives in several floras. They are of the nature of vicarious species such as *Abies nobilis*,



*A. magnifica*, and *A. shastensis* in one vicarious lineage, and *A. concolor*, *A. arizonica* and more remotely, *A. grandis* and *A. lasiocarpa* in another such lineage. Similarly, *Pinus ponderosa*, *P. scopulorum*, *P. Jeffreyi*, and *P. washoensis* constitute one vicarious lineage and *P. contorta*, *P. Bolanderi*, *P. Murrayana*, and possibly also *P. Banksiana* constitute another. The redwood stands alone as the sole survivor of its Tertiary lineage and taxonomically seems indistinguishable from the fossil *Sequoia Langsdorffii*. *Abies bracteata* is likewise a sole survivor of a divaricate lineage that once reached central Oregon and southern Colorado and was represented by the fossil species *A. Chaneyi* and *A. longirostris*. Every genus of plants that is elaborated over western North America comprises one or more such genetic lineages. Where and when any of these lineages happened to have associated itself with the redwood, it became technically a part of the redwood association. By reason of the fact that the redwood apparently once occupied an area from the Pacific Coast through the Rocky Mountains, most of these lineages have been associated at some time, in at least some of their taxonomic aspects, with the history of the redwood. Today, however, the present floristic expression of these lineages occurs in associations that comprise a series of floras occupying distinct geographic areas, each having more or less obvious environmental differences, each with a characteristic floristic composition, and each occupying a segment of the area that once was the home of the redwood. Using very broad terms for these floras, we may speak of them as the Rocky Mountain forest, the Sierra Nevada forest, the North Coast Douglas fir forest, the black oak-madrone forest, and the modern redwood forest. All of them appear to have developed in part, through by no means completely, from genetic lineages that have had a considerable history of association with the redwood floras of the Tertiary. The segregation of these into separate floras must be interpreted in terms of environmental influences inviting selection and segregation of genetically developing, interbreeding, independent populations. Today, the obvious thread of relationship is through the distribution pattern of vicarious species, a pattern of lineage that must have been very real as it developed through the past.

We can begin the discussion of each of these floras in the order of the closeness of their relationship to the modern redwood forest. Therefore, we will discuss the black oak-madrone forest and the North Coast Douglas fir forest first and the more remote Sierra Nevada and Rocky Mountain forests last.

If we should remove the redwood from the modern redwood forest, the aspect of the resulting flora in the northern part of the distributional area would fit well into the northwest Douglas fir forest. If we should remove much of the Douglas fir, as well as the redwood, the forest over much of its southern and central area would fit perfectly into Cooper's (1922) concept of the black oak-madrone forest. To remove the redwood or the Douglas fir by natural means

would necessitate certain changes in environmental conditions that would exercise environmental selection on the species population. This has happened in the past as is very evident from the fossil record, and both the black oak-madrone forest and the North Coast Douglas fir forest, with certain additions and genetic changes made possible by the changed conditions, developed independently largely out of the redwood forest. Here are cases of environmental selection operating on the migrating species populations that constitute what we term a flora. This selection is made possible, on the one hand by variations in the range of tolerances to the various environmental factors among the various species, and on the other, by genetic changes in the constitution of certain of the species, resulting in physiological races that become segregated in the various forest assemblages. Along with this situation has occurred the extermination of other species either completely or locally that opened the area to expansion for some of the species remaining and to immigration of others from the outside.

The black oak-madrone forest is essentially a redwood border forest occurring chiefly on the southern and eastern borders of the redwoods where the relative humidity receives much less benefit from the recurrent summer fog than it does in the redwood forest. This broad-leaf forest is characteristic of the region from the Santa Lucia and Santa Cruz mountains of California to the southern Cascade Mountains of Oregon. It occurs at low altitudes in equable temperatures. It contains few species not found somewhere in association with the redwood. According to the fossil record, the black oak-madrone forest began its development in Miocene time as a result of increased aridity. Chaney (1925) points to significant changes in this direction in the Mascall flora of Oregon. Most of the modern woody species can be traced through probable genetic lineages well down into the Tertiary redwood forest. Along with the diminution and subsequent loss of the redwood from the flora, we see also the disappearance of many other plant species through extermination. This is especially true of the so-called Asiatic "element," such as *Ginkgo*, and *Cercidiphyllum* which formerly occurred in the flora of Pacific North America. We may conclude, inasmuch as this forest is composed of members with physiological requirements close to those of the redwood forest, that in spite of the antiquity of its divergence it has not progressed far from that forest.

Judging from the extent that the characteristic species of the northwest Douglas fir forest overlap into the redwood flora, it may likewise be considered closely related ecologically and floristically to the redwood flora. As an independent flora it occurs chiefly north of the redwood area. Within the redwood area, the Douglas fir occurs also at higher altitudes, a fact which suggests that it may have tolerances of lower temperature extremes. The Douglas fir forest elements began increasing in importance within the redwood forest in middle Tertiary time. By Pliocene,

over much of the area of the redwood, Douglas fir was a very important member of the forest along with Thuja, the spruces (Picea), and the firs (Abies). Pleistocene cooling in all probability served as a sharp impetus to the restriction of the redwood and to the high development of the Douglas fir forest in medium latitudes and medium altitudes. There are few tree species characteristic of this modern flora not represented by genetic lineages in the Tertiary redwood forest as represented in the known fossil floras. Some of the lineages, however, have had a considerable prior history on the continent both to the south and to the east.

The upland conifer forest of the Sierra Nevada is likewise to be regarded as representing the end points of genetic lineages that have had some of their development along with the Tertiary redwood forest. Some of this historic association has been recent and some more remote. Here, however, there appear to be two or three distinct patterns of coincidental restriction of area which suggest that different sets of environmental forces or at least different total coincidental tolerance spans of the component species were involved. One such group is confined to the California flora and is typified by the distribution pattern of such Californian endemics as *Pinus Lambertiana*, *P. Jeffreyi*, *Abies magnifica*, *Libocedrus decurrens*, and *Sequoiadendron giganteum*. Except for the *Sequoiadendron* these plants appear to have had an intimate contact with the coast redwood forest at least as far back as middle Miocene time, and during Pliocene time comprised a conspicuous element of the redwood flora of the coast ranges. There is by no means a complete coincidence of area of these species since they divide today into two overlapping altitudinal groups involving the Jeffrey pine and the fir on the one hand and the sugar pine and incense cedar on the other. The *Sequoiadendron* lineage has been reported by Axelrod (1944, p. 121) from the upper Miocene of Coal Valley in western Nevada. It was not there in association with a coast redwood flora and there is doubt that it ever was. A lineage of apparently similar interior history is reflected by *Pinus Balfouriana* of the south Sierra Nevada and *P. aristata* of the southwest plateau. Another large element of the Sierran forest belongs to a series of complex lineages whose present representatives appear to contribute to much broader tolerance spans. There seems little doubt from the nature of their occurrences that the representatives in the Sierra Nevada comprise local genetic races with tolerance spans today similar to those of the sugar pine and the Jeffrey pine. Elsewhere their members, or closely related vicarious representatives, constitute the bulwark of the Rocky Mountain forest flora. Furthermore there are vicarious relatives in the maritime floras of the northwest, in association with species vicarious between the coastal area and the Rocky Mountains but not represented in the Sierra Nevada. This widespread element of the flora is typified by the species discussed below. *Pinus ponderosa* occurs in the Sierra Nevada and sporadi-

cally in the coast ranges of California. It extends northward in the Cascades. In the Rocky Mountain forest it is represented by the closely related vicarious species *P. scopulorum*. *Pinus monticola* occurs as distinct ecotypes with local minor bark differences throughout the upper part of the flora of the Sierra Nevada, in the Cascade Range and in the Rocky Mountains. In the Puget Sound region there occurs a coastal race. *Pinus Murrayana* is represented by distinct ecotypes in the Sierra Nevada and the Rocky Mountains with a closely related vicarious member, *P. contorta* in the maritime floras of the Northwest. *Abies concolor* occurs both in the Sierra Nevada and the Rocky Mountains. A closely related form, *A. arizonica*, occurs in the Southwest and another vicarious relative, *A. grandis*, occurs in the maritime flora along the coast.

It would seem, then, that historically the flora of the Sierra Nevada has had both recent and more remote lineal associations with the older Tertiary floras of the north as well as with interior and possibly southern floras. Some of the so-called endemic element in part segregated out in Pliocene and Pleistocene time from the redwood flora in response to progressively increased aridity and cooling, and in part filtered in from upland floras that occupied the highlands of this western area (the Madro-Tertiary Flora of Axelrod). The more widespread elements developed from lineages more closely related floristically to the Rocky Mountain flora whose relationships will be discussed presently.

The Rocky Mountain forest inhabits an area of high relief with a climate that is markedly continental in character. There are frequent summer thunder showers and very cold winters. It is flanked on the west by the arid Great Basin and on the east by the semi-arid great plains. Many of its vicarious relationships with the Sierra Nevada forest and the maritime forest of the northwest coast have been discussed. A few more need to be taken up. These involved genetic lineages between the North Pacific coast maritime floras that do not occur in the Sierra Nevada and lineages in common with the southwest plateau and southern Great Basin. The spruces do not occur in the Sierra Nevada. A genetic lineage involving *Picea pungens* and *P. Engelmanni* of the Rocky Mountains and *P. Breweriana* of the north coast ranges of California and *P. sitchensis* of the maritime floras of the northwest coast seems to have had a long history in conjunction with the Tertiary floras of western America. Isolated stands of *Picea Engelmanni* in the Cascades attest the past wanderings of this lineage. Much of this lineage appears to have been with the redwood flora. No doubt more of it extended into upland floras above the redwood forest. In the southern Rocky Mountains are representatives of two coniferous lineages that have elaborated themselves over the entire southwest plateau and southern Great Basin. These are the *Pinus cembroides* complex and a large segment of the genus *Juniperus*. Neither of these lineages appears to have had much, if any, of a northern history although

a so-called *Juniperus scopulorum* occurs in the maritime flora of the Puget Sound area in a wet land habitat that suggests considerable physiological departure from its interior counterpart.

### SUMMARY AND CONCLUSIONS

I have attempted to point out that floristic history must be interpreted from the point of view of the interactions of the three phases of vegetation dynamics, namely: (1) the environment, including its spatial variation, its fluctuation and the history of its changes; (2) the physiology of the individual organisms, especially as reactions are attuned to environmental conditions, as these may be integrated within the individual, and as they may vary between individuals; and (3) the genetics of the population, noting especially the building up or the depletion of genetic diversity within the population, especially as these phenomena affect the range of variation of tolerances and the development of new genetic races. I have further pointed out that such dynamics leave little room for concepts of vegetation in time or space that regard the community as a functioning unit made up of wholly interdependent individuals. The interdependencies within the community are strictly within the sphere of parasitism and symbiosis and as such are the special problems of special cases. The functional unit within the community is the interbreeding population. It provides the mechanism of continuity, of migration and of adaptive change. The association of any two or more such populations in any community results from coincidence, due, on the one hand, to events of history and on the other, to the coincidence of tolerances of the overall environmental factors.

To trace the developmental histories and the interrelationship of floras demands the exercise of judgment that appreciates the limitations that can be expected of vegetation dynamics, of what is possible in environmental relations, physiological reactions and genetic processes. Of the facts that are available to us, ideally the fossil record should provide us with the most reliable information. Unfortunately the fossil record as revealed to us is so discontinuous and incomplete and fraught with misidentifications, as to be very unreliable as a means of developing even the framework of the story. The story must be pieced together from facts drawn from several sources. Probably the cornerstone should rest on the distribution patterns of vicarious species as these are asso-

ciated with other vicarious lineages today and through time. From this point interpretation must follow the pattern of phylogenetic history and evidences of physiological and environmental change. The fossil record from time to time may serve to substantiate or to reject interpretations and to embellish the story with local details.

Applying such ideas to the relationships of the floras of western North America there is evidence of much parallel phylogenetic history among the genetic lineages that make up the forest flora of the redwood forest, the black oak-madrone forest, the North Coast Douglas fir forest, the upland conifer forest of the Sierra Nevada, and the Rocky Mountain forest. These lineages have come together from many sources and represent the interlacing of divaricate and reticulate patterns whose present day occurrences may be interpreted as a segregation of genetic lineages through the interaction of environmental conditions on physiological processes. The fossil record of this story is badly in need of taxonomic reevaluation by experts in the various groups of plants represented.

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DEVELOPMENT OF THE DECIDUOUS FORESTS  
OF EASTERN NORTH AMERICA

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IN A SYMPOSIUM ON  
ORIGIN AND DEVELOPMENT OF NATURAL FLORISTIC AREAS  
WITH SPECIAL REFERENCE TO NORTH AMERICA

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## DEVELOPMENT OF THE DECIDUOUS FORESTS OF EASTERN NORTH AMERICA

### INTRODUCTION

The deciduous forest formation of eastern North America is a complex vegetational unit most conspicuously characterized by the prevalence of the deciduous habit of most of its woody constituents. On a basis of dominant species, four major climax associations are distinguished: *mixed mesophytic*, centrally located; *oak-hickory*, in general to the west and southwest; *oak-chestnut*, to the east and southeast; and *beech-maple* to the north, north of the Wisconsin glacial boundary.

Since the climax association is an abstract concept (cf. Cain, this symposium) based upon familiarity with numerous concrete examples, each differing in minor details from one another, its delimitation in space is difficult if not impossible. The respective positions of the several associations can be shown diagrammatically, but they cannot be mapped unless one wishes to map the location of each forest stand which meets the specifications of the concept.

On the other hand, it is entirely possible to recognize forest regions which are characterized by the prevalence of specific climax types, or by mosaics of types. These are natural areas as defined by Cain.

### FOREST REGIONS OF THE EASTERN UNITED STATES

The present pattern of distribution in terms of forest regions, of which I recognize nine in eastern United States,<sup>1</sup> is somewhat as follows:

1. The *mixed mesophytic forest* region, centrally located, and occupying much of the unglaciated Appalachian Plateau. It is characterized by the prevalence of mixed mesophytic climax communities, which reach their best development in the Cumberland Mountains (Braun 1942).

2. A *western mesophytic forest* region, between the mixed mesophytic forest region and the bluffs of the Mississippi River. It includes the Interior Low Plateau and some contiguous areas. Its vegetation is a mosaic of unlike climaxes and subclimaxes.

3. The *oak-hickory forest* region, centering in the Interior Highlands (Ozark and Ouachita mountains) and extending northward and northeastward onto glaciated territory.

4. The *oak-chestnut forest* region, including most of the Ridge and Valley and Blue Ridge provinces, and extending across the Piedmont onto the Coastal Plain from northern Virginia northward. It is characterized by the dominance of oak-chestnut forest on most of its slopes, and of white oak forest particularly on the broad expanses of the Great Valley.

5. The *oak-pine forest* region, which might be called an eastern oak-hickory region. It occupies most of the Piedmont Plateau from Virginia southward and stretches across the Gulf States as a transition belt between more northern and more southern regions.

6. The *southeastern evergreen forest* region, which includes some deciduous forest communities.

7. The *beech-maple forest* region, lying to the north of the mixed mesophytic and western mesophytic forest regions. Its southern boundary is the southern boundary of Wisconsin glaciation.

8. The *maple-basswood forest* region, the most northwesterly region of deciduous forest.

9. The *hemlock-white pine-northern hardwoods* region, generally considered as a distinct formation, stretches across the north.

Each of these forest regions has undergone a different history. I shall endeavor to present a chronological account<sup>2</sup> of this eventful history, although I am fully aware of the hazards and uncertainties attendant upon building up such a picture from the inadequate evidence at hand. However, such an attempt may stimulate investigations which will add further evidence.

### HISTORICAL BACKGROUND

The history of deciduous forest in North America dates back many million years to the latter part of the Mesozoic era. Events previous to that time determined the nature and extent of the continent on which forest development was taking place.

The Appalachian Revolution at the close of the Paleozoic era was a time of mountain making in the East. All of what is now known as "Appalachian Highland" then became highland. Then, too, the Ozark area was uplifted to a height of several thousand feet. In the West (Cordilleran area) the land was low-lying with large epicontinental seas. The extent of continental eastern America in the early Mesozoic may have been comparable to that of the present. Erosion began its work of reducing the great mountains formed during the Appalachian Revolution. The earliest record of Mesozoic erosional history in the East is that preserved in the Fall Zone peneplain, a seaward-sloping surface older than Cretaceous. Sinking of the Fall Zone peneplain took place in time for it to receive Cretaceous sediments. The seacoast then was somewhere within the present limits of the Appalachian Highland, landward of the present margin of Cretaceous deposits.

<sup>2</sup> This account is greatly condensed from Part III of the writer's forthcoming book, "Deciduous Forests of Eastern North America." Physiographic interpretations follow Fenneman, 1938. Because so condensed, some statements may appear to have a more precarious foundation than is actually the case.

<sup>1</sup> In a forthcoming book, "Deciduous Forests of Eastern North America."

of the Coastal Plain, and perhaps close to the Allegheny-Cumberland Front; it extended up the Mississippi Embayment to or beyond the mouth of the Ohio River. Meanwhile, the epicontinental seas of the Western Interior had increased in size and the sea had entered from the Gulf covering a wide belt east of the Rocky Mountains. The Ozark Highland was connected with the East.

In the sediments then being deposited, are found the records of plant life<sup>3</sup> of that period, of the forests which inhabited the then low-lying and small continent.<sup>4</sup> Late in the Lower Cretaceous period, angiosperms appeared in the American record. Even from the beginning of the record in America, a few forms referable to living genera and many others with considerable similarity to modern genera occurred. A little later, the representation of modern genera was such as to definitely establish the presence of broad-leaved forest communities.

In the Upper Cretaceous period, the abundance of diot fossils in eastern deposits indicates that by that time broad-leaved forest had become dominant in eastern North America. Among the genera still living in our deciduous forest which are represented in deposits of the Atlantic slope and Mississippi Embayment may be mentioned *Acer*, *Fagus*, *Quercus*, *Liriodendron*, *Magnolia*, *Juglans*, *Celtis*, *Populus* and *Salix*. Gymnosperms also were present, among them representatives of genera which we now think of as northern (*Picea*, *Thuja*); and others, of which *Torreya* should be mentioned, as it still maintains an isolated station on the Coastal Plain. A number of genera which have since retreated to the Tropics or the Southern Hemisphere were then included in the North American forests.

Uplift then took place. The emergent plain, covered with Cretaceous sediments, was the beginning of the Coastal Plain.<sup>5</sup>

The Coastal Plain, exposed for the first time, was wider than the present band of Cretaceous outcrop. Its inner margin corresponded with the seacoast of Cretaceous time, somewhere on the "Appalachian Highland." The vast Cretaceous epicontinental sea of the Western Interior was reduced in size and continuity, and ocean connections broken. The water barrier between Atlantic America and Mexico was removed, thus opening up a route for migration to and from low latitudes. New land areas were available for vegetational occupancy; the old land area was again raised to highland status.

The nature of the vegetation cover of the low-lying coastal region is incompletely recorded in the early Tertiary deposits of the Coastal Plain and Mississippi Embayment. The Wilcox flora (of which Dr. Chaney has spoken in this symposium) contained

many genera with representatives today in inland or upland forests of the warmer parts of the Temperate Zone and in the Tropics, and some genera with modern representatives in the American deciduous forest. Among the later may be mentioned *Aralia*, *Aristolochia*, *Asimina*, *Bumelia*, *Celastrus*, *Carya*, *Cercis*, *Cladrastis*, *Cornus*, *Diospyros*, *Fraxinus*, *Ilex*, *Juglans*, *Liquidambar*, *Magnolia*, *Nyssa*, and *Taxodium*. This flora contrasts strongly with that of the Upper Cretaceous; it is much more southern in character and lacks the common Holarctic genera of the earlier flora.

In the Western Interior, the Raton, Denver and Fort Union floras (floras of which Dr. Chaney has also spoken) demonstrate latitudinal influences. These floras show a decrease in subtropical genera from south to north, and a corresponding increase in temperate genera.

Latitudinal and no doubt altitudinal variations in forest composition of early Eocene eastern forests existed, just as is demonstrated in the western interior. Even if the differences between the Eocene floras of the coastal strip and the contemporaneous Eocene floras of the Appalachian Highland were no greater than exist today between the forests of the Coastal Plain and Appalachian Highland, it could confidently be asserted that in Eocene time a hardwood forest, containing a large proportion of the existing genera of our deciduous forest, clothed the upland.

While some record of lowland vegetation was being preserved near the coast, the inland areas were being constantly modified by erosion. Progress in the erosion cycle initiated by post-Cretaceous uplift at first increased topographic diversity due to dissection of the upraised peneplain. Later, as old age in the cycle was approached, as more and more of the land again became reduced to peneplain status, those plant communities favored by topographic diversity of maturity in the cycle became restricted; those which found the poor drainage of a peneplain or the acid swamps of sandy low plateaus most favorable, expanded. Meanwhile, the Coastal Plain was growing and a coastal plain flora was developing, a flora derived in part from migrations from the Appalachian Highland, in part from migrations from lower latitudes.

This cycle of erosion culminated in Miocene time, in the Schooley peneplain, the oldest surviving peneplain, and the most complete of which there is record.<sup>6</sup> Perfection of the Schooley peneplain must

<sup>3</sup> While the exact time at which the Schooley cycle was interrupted by uplift is open to question, it is (according to Fenneman 1938) "doubtful that it was raised enough for erosion to begin cutting it away before the end of the Miocene." While a large part of the area had doubtless reached peneplain status earlier, much of the area did not feel the effects of rejuvenation until later. In fact, some areas are still undissected. The extent of the Schooley peneplain (and its correlatives) is a matter of concern in the interpretation of forest history. Certainly it affected the entire Appalachian Highland. It must have developed farther west, over the Interior Low Plateau. As its surface everywhere declined toward the coast and toward major streams still in existence, it sloped westward to the Mississippi Embayment. As later peneplains also declined toward the Mississippi, the Schooley and later surfaces finally converged or almost converged. The ridges which have survived a later peneplain (the Lexington) probably survived also on the Schooley (Cumberland)

<sup>3</sup> Paleobotanical information mostly from Berry 1914, 1916, 1916L, 1919, 1924, 1925, 1930, Clements and Chaney 1936, Elias 1935.

<sup>4</sup> If the superposition hypothesis is accepted, the Appalachian Highland was reduced in size approximately to what is now Appalachian Plateau (Fenneman 1938, p. 258, 259, Johnson 1931).

<sup>5</sup> There may have been a cycle of erosion which ended in a Cretaceous peneplain. The Fall Zone peneplain is older than Cretaceous, the next peneplain of which there is positive evidence is younger than Cretaceous. The so-called "Cretaceous peneplain" of earlier writers is younger than Cretaceous.

not be overestimated. Remnants of the peneplain where it was best developed indicate a relief of several hundred feet in 40 or 50 miles. In the Blue Ridge of Virginia, knobs and swells reached a thousand feet above the peneplain surface. In the Southern Appalachians, subdued mountains several thousand feet in height remained. The Cumberland Mountains retained considerable relief. In fact, wherever in the Appalachian Highland resistant rocks outcropped, smoothness of the land surface was interrupted, and some topographic diversity maintained. This was true in the Adirondack and New England mountains as well as southward, but there glaciation destroyed all previous vegetation and no pre-Pleistocene correlations can be made.<sup>7</sup> The plants and plant communities of hilly and mountainous lands were of necessity restricted to these places.

In this connection I wish to call attention to three features of forest distribution which I believe to be significant. These are:

(1) The finest areas of mixed mesophytic forest occur in those places where the Schooley peneplain was never perfected, namely, in the Cumberland Mountains, along the western edge of the Cumberland and southern Allegheny plateaus, and in coves of the Southern Appalachians.

(2) Mixed mesophytic forest prevails over the great area where the upland levels represent the reduced Schooley peneplain, and where no later peneplain was extensively developed, that is, over the southern half or more of the unglaciated Appalachian Plateau.

(3) Relic disjunct mixed mesophytic forest communities occur almost everywhere that isolated remnants of the Schooley peneplain are found, except to the east of the Allegheny and Cumberland fronts. (Advance disjuncts are the rule in that direction.)

I have felt it necessary to assume that there is a cause and effect relationship. Not only are there distributional correlations with early and middle Tertiary physiography; the large array of Tertiary genera, the many now highly local disjunct and endemic forms of these areas, can only be explained on a basis of Tertiary history and development of the Schooley peneplain. The mixed forest of the Tertiary became restricted to areas of diverse topography; to these areas, too, many of the ancient forms (with relatives in Asia) retreated as peneplanation rendered large areas unsuitable for their continuance. Thus today they exhibit relic distributions correlated with these always unreduced areas of the Schooley peneplain (for example, *Rhododendron Catawbiense*, *Stewartia pentagyna*). It is almost certain that a

vegetation comparable to that of the Coastal Plain spread over the flats of the peneplain, especially where that was developed on acidic rock. For evidence, note the relic distribution of what we now call coastal plain plants, and of colonies of coastal plain plants, on the relatively unmodified remnants of the peneplain, swampy un rejuvenated stream heads or sandy plateaus dotted with low monadnocks (Braun, 1937a, b). Further evidence of antiquity is afforded by such rare endemics as *Buckleya distichophylla* (parasitic on the roots of hemlock), which belong to families now largely tropical or subtropical in distribution, and which must date back to the period of supremacy of subtropical forms in southern United States; or, by our climbing fern, *Lygodium palmatum* (abundant along the western margin of the Cumberland Plateau), which genus today is mostly tropical and which was common in the Middle Eocene. When, later, elevation took place and dissection of the peneplain began, the mixed forest again expanded but many of the restricted species were no longer able to extend their ranges. They are the relic disjuncts of today.

#### MIXED FOREST OF THE TERTIARY AND ITS DERIVATIVES

##### OLD PENEPLAINS AND THEIR DISSECTION

The progenitor of what we now call Mixed Mesophytic Forest was present in Miocene time, or even earlier, and has continued to the present.

Uplift of the Schooley peneplain in late Miocene time initiated the Harrisburg cycle of erosion, a cycle which consumed only a fraction of the time of the Schooley cycle. The weak rocks to the east were rapidly reduced. The Great Appalachian Valley became a major topographic feature. Longitudinal ranges formed on resistant siliceous rock stood above the valley. The Piedmont Plateau was reduced. The infertile soils derived from the resistant rock of the ridges, and the shallow soil over the steeply inclined strata are not (and doubtless were not) favorable to a mixed mesophytic forest. Oaks and chestnut probably then gained ascendancy, and have kept it except where erosion in the present cycle has produced habitats favorable for the invasion of species of the mixed mesophytic forest.

The Schooley peneplain over the resistant rocks of the Appalachian Plateau was not destroyed,<sup>8</sup> although the extent of rugged land was increased by dissection, and thus the extent of land suitable for mixed mesophytic forest was increased. Westward over the Interior Low Plateau, the extensive development of the Lexington peneplain (more or less equivalent to the Harrisburg of the Atlantic slope) profoundly modified topography except in certain areas and is in part responsible for the mosaic of vegetation types there seen.

<sup>8</sup> Lower levels do exist; a younger peneplain, designated as "Allegheny" by some, and here (following Fenneman) considered as more or less equivalent to the Harrisburg, is evident in West Virginia and eastern Ohio. The mixed oak forest which here interrupts the mixed mesophytic forest may date from this time. The western edge of the Allegheny Plateau retained its Schooley level (reduced) as did most of the Cumberland Plateau.

peneplain. The rugged areas still apparent are Muldraugh's Hill, the hills along the Dripping Springs escarpment, and a height of land roughly connecting the two and lying north of the Green River in Kentucky. In the Ozark and Ouachita provinces, an older and a younger peneplain are distinguished. Only the Boston Mountains in the Ozarks, and Rich Mountain in the Ouachitas remain to indicate the old surface, which may be more or less equivalent to the Schooley peneplain of the Appalachian Highland.

<sup>7</sup> For this reason, pre-Pleistocene history of the glaciated area is omitted from this account.

## THE WESTERN INTERIOR

Meanwhile, in the Western Interior, increasing aridity (due to the interception of moisture-bearing winds from the Pacific by the rising Rocky Mountains) reduced the forest vegetation. The plains came to be occupied by grassland (indicated in the fossil record by the abundance and diversity of grazing mammals, and by the remains of a number of grasses). A continental climate and a pattern of distribution of vegetation types similar to that of the present were initiated. The mixed deciduous forest was forced to retreat eastward from the drying interior; the more mesophytic forest species retreated<sup>9</sup> farther to the east than did those of lower moisture requirements. The Ozark and Ouachita mountains contain relic communities of mixed mesophytic forest in the two rugged areas (Boston Mountains and Rich Mountain) whose summit elevations represent the old peneplain surface; elsewhere, oak and oak-hickory forest prevail.

## EXPANSION OF THE OAK FOREST

At the same time that climatic conditions restricted the mixed forest to areas of diverse topography with compensating effects of microclimates and slightly higher rainfall due to condensation in an unstable column of air, the expansion of oak forests over the contemporaneous Harrisburg peneplain and its correlates was favored. Oak forests now occupy much of these levels in the Great Valley, the Piedmont Plateau, and enter into the mosaic pattern of the Interior Low Plateau. Due to the peculiar reactions of an occupying oak forest upon the soil, continuance of the oak type is favored until such time as new soils are formed as a result of stream rejuvenation.

## THE COASTAL PLAIN

The Coastal Plain, from the time of its first emergence as a result of post-Cretaceous uplift to the end of the Tertiary, was gradually enlarging. New land areas onto which vegetation could expand were continually being formed. In places where age, elevation, or lithological character of the substratum favored diversity of topography and development of fertile soils, mixed mesophytic communities occur, always with a pronounced admixture of more southern species, as *Magnolia grandiflora*. Such areas, in part at least, are above the level of Pleistocene submergence. Their forests are indicative of Tertiary expansion, not Pleistocene migration.

## THE PROBLEM OF THE PLEISTOCENE

Pleistocene glaciation enters the picture. With the growth and advance of ice caps the vegetation of the North was destroyed. Northern plants migrated southward in advance of the ice (in response to climatic change), invading the established vegetation insofar as suitable habitats were available or weakened competition of more southern forms permitted.

To and fro migrations took place, not once, but

<sup>9</sup> Fossil records show that the common genera of mesophytic forests (as *Fagus*, *Acer*, *Tilia*, *Aesculus*, *Fraxinus*, *Castanea*, *Asimina*) were present in the Western Interior in early Tertiary (Fort Union formation).

with each advance of ice. Vegetational occupancy of glacially denuded land in the interglacial stages is positively shown by plant remains in interglacial deposits. Migrations following the retreat of the last ice sheet have determined the nature of the vegetation of all the area covered by that ice sheet.

One of the biggest problems in connection with Pleistocene vegetation is the extent to which the vegetation south of the ice margin was affected by glacial climate, or was modified by invasions of more northern plants. Two lines of evidence are available:

(1) Fossil evidence, including postglacial pollen records preserved in bogs south of the glacial boundary, and plant fragments preserved in proglacial lake, fluvial, and estuarine deposits.

(2) Evidence afforded by present distribution of species, disjunct occurrences, and the like.

From fossil evidences we may conclude that nowhere far beyond the glacial boundary was climate during the glacial stages sufficiently severe to displace occupying vegetation. Such infiltration of northern species as is demonstrated in certain instances by pollen records or plant fragments was made possible in part by slightly cooler climates, in part by the lack of competition on newly exposed Pleistocene coastal terraces and on fluvial deposits.

In interpreting the fossil evidence,<sup>10</sup> which is almost entirely from the Coastal Plain, we must keep in mind that the great mass of coastal plain vegetation is still in developmental or subclimax stages; few climax communities occur. Only in the climax do vegetational reactions tend to exclude invaders; developmental stages are constantly changing and the opportunity for extra-regional invaders to enter is far greater than in climax communities. Migration southward on the Coastal Plain was facilitated during each glacial advance by the withdrawal of the sea (water locked up in glacial ice) which resulted in a continuous similar habitat from the glacial margin southward to the Gulf along which rapid migration could take place. In the Mississippi Valley, the overloaded stream of glacial stages built up many bare areas open to invasion from the north. Microclimates may have played a part. Evidence from a Texas bog is most difficult to interpret in the light of pres-

<sup>10</sup> Evidence from fossils is conflicting. No fragments of northern plants are known from Pleistocene deposits of the Atlantic Coastal Plain. However, it is possible that all of these deposits are interglacial in age. All indicate the continuance through the Pleistocene of forest vegetation comparable to that of coastal areas today. On the other hand, Brown (1938) has found remains of white spruce, larch, and northern white cedar in river terrace deposits in Louisiana, but always in association with southern plants, plants now in that latitude. Pollen records from bogs in unglaciated southern New Jersey (Potzger 1945) show an infiltration of northern species in the lower levels of the bogs, especially in those closest to the glacial boundary. But, at the same time that fir and spruce were present, chestnut and sweet gum were also present; in general the forest was about the same throughout the time that peat accumulated. A North Carolina bog record (Buell 1945, 1946) indicates a stronger infiltration of northern trees in the early part of the record, including *Abies* and *Pinus Banksiana*. In a Texas record, *Abies*, *Picea glauca* and *P. mariana* are represented in small percentages, along with pine (species not suggested), alder, oaks, and grasses, and at some levels, hickory, chestnut and *Tilia*. The chestnut, which reached a maximum after the spruce and fir, indicates a climate more humid than the present (Potzger and Thorp 1943, 1946). Records from the Dismal Swamp of Virginia (Lewis and Cooke 1929, Cooke, Lewis and Patrick 1934) show no infiltration of northern species, but rather demonstrate successional development from open marsh to closed forest.



ent knowledge. Glacial anticyclones, and plains "northers" similar to but more extreme than those of the present are possible factors.

Almost all of the records, however, are in marginal positions, and give little or no evidence as to glacial influences in the Appalachian Highland and Interior Low Plateau. For this extensive area, the evidence afforded by species and community distribution is all that is available. The time at my disposal does not permit more than an outline, with examples, of the vegetational features of significance in connection with migrations (or lack of migrations) south of the ice sheet in the eastern interior during the Pleistocene.

(1) Position of and nature of northern boundaries of species ranges and of communities with reference to the glacial boundary. For example: The two most characteristic species of the Mixed Mesophytic forest, *Tilia heterophylla* and *Aesculus octandra*, are abundant to the glacial boundary and into the area of Illinoian glaciation, but have scarcely invaded into the area covered by Wisconsin ice. There is a distinct boundary between mixed mesophytic and beech-maple forest correlated with the Wisconsin glacial boundary.

(2) Nature and composition of different parts of communities occupying continuous environments extending in north-south lines away from the glacial boundary. For example: the rugged western margin of the Appalachian Plateau harbors excellent mixed mesophytic forest which is as rich in species in all layers near (not at) the glacial boundary as it is 200 miles farther south. The same area contains southern disjuncts, highly local species, endemics, and species whose disjunct ranges correspond with the unreduced remnants of the Schooley peneplain. The white oak forest of the valley floor of the Great Valley (Harrisburg peneplain) is essentially the same in Pennsylvania as in southern Virginia.

(3) Contrasts between the vegetation of areas flooded by ponding of streams during early Pleistocene ice advances and adjacent nonflooded areas, and the disjunct occurrence of southern species along such pre-glacial drainage lines. For example: Mixed mesophytic communities are largely displaced by oaks in the ponded areas. A considerable list of species has been compiled, which (in southern Ohio) are limited to elevations above the level of proglacial lakes;<sup>11</sup> some of these (as *Styrax grandifolia*, *Chionanthus virginica*, *Magnolia macrophylla*) are decided disjuncts.

(4) The more southern mountain or plateau bogs and swamps generally harbor coastal plain relics and very few if any mildly northern forms. For example: The relic communities in unrejuvenated stream heads on the southern part of the Schooley peneplain.

(5) Relic occurrences of northern communities and species. For example: Typical northern bog communities occur as far south in the Alleghenies as

West Virginia (Cranberry Glades is one of these). Relic occurrences of *Thuja* and *Taxus* on cliffs near the glacial boundary west of the mountains; of *Abies balsamea* in the Alleghenies of West Virginia and the Blue Ridge of Virginia; of *Betula lutea* var. *macrolepis* in ravine box-canyons tributary to the Green River above the level of Pleistocene alluviation. The so-called northern disjuncts on the Gulf Coastal Plain are not here regarded as of Pleistocene origin.<sup>12</sup>

There is abundant evidence of persistence of southern forms and communities not far from the ice front. Some lowering of altitudinal belts in the mountains is indicated which permitted southward migration of northern vegetation. There is little evidence that this extended south of West Virginia along the Allegheny-Cumberland axis, nor south of Virginia in the Blue Ridge.<sup>13</sup> Away from mountain axes, there is some indication of local infiltration of northern species.

Fossil and vegetational evidence both indicate that the deciduous forest was not displaced south of the glacial boundary, except in a band of varying width along the ice front. The width of this band may have been affected by elevation, by direction of drainage (toward or away from the ice front) and by the direction of prevailing winds and winds off the ice. The severity of freezing effects such as have been noted in certain periglacial soils may be helpful in determining the extent of climatic shift.

#### POSTGLACIAL MIGRATIONS

The postglacial migration of forests onto the area covered by Wisconsin ice is recorded in pollen spectra of bogs, and is so well known that it need not be discussed here except in its broadest implications. The long-continued dominance of spruce in the southern part of the area of Wisconsin glaciation (Potzger 1946) indicates a broad band of northern conifer forest on the new land, and slow displacement by deciduous forest invaders (Transeau 1941). This may be correlated with the slow and halting retreat of the ice which is indicated by the several recessional moraines. The inference that an equally broad band of conifers existed south of the ice margin does not follow; many other factors are involved. The xerothermic period (indicated in some pollen records) permitted rapid eastward spread of oak-hickory forest into the area known as the Prairie Peninsula; in much of that area, oak has retained its dominance to the present. The order of appearance of pollen of certain of the deciduous forest genera is a basis

<sup>12</sup> These are located in the Tallahassee red hills, Marianna red lands, Apalachicola River bluffs in northern Florida, and in the Tunica Hills of Louisiana and Mississippi (Harper 1914, Kurz 1928, 1930, Brown 1938). Their most distinctive feature is their mixed deciduous forest. The presence in one of these areas (Apalachicola River bluffs) of two endemics of ancient ancestry, *Torreya taxifolia* and *Taxus floridana*, both widely separated from other species of their genera, indicates that these communities are older than Pleistocene; the beech of this area may be genetically distinct (*sic* Camp), thus indicating a longer period of isolation.

<sup>13</sup> The Southern Appalachian fir (*Abies fraseri*) is distinct from the northern fir. Since the earliest ice advance reached farthest south in the east, there is a possibility that the first wave of migration reached this far south, and that species segregation has since resulted.

<sup>11</sup> See Rich (1934) for earliest account of these lakes; Transeau (1941) and Wolfe (1942) for effect on vegetation.



for postulating time and direction of migration (Sears 1942).

#### CLIMAX ASSOCIATIONS OF THE GLACIATED AREA

The climax associations of the glaciated area owe their origin to postglacial migrations. Their boundaries have not yet reached a position of climatic equilibrium. The lobe of oak-hickory forest entered early, soon after the period of spruce dominance. The mass invasion probably came from the Ozarkian center (established in Pliocene time), although some invasion of oaks may have come from mixed forests south of the glacial border. Their early entrance in all profiles indicates this. Furthermore, a number of species of oak are able to occupy sites unsuitable to climax mesophytes and establish long-enduring developmental stages which retain dominance until topographic and soil development permits successional advance and the dominance of more shade-tolerant species. This is particularly true on the till plains of the Central Lowland, where ultimately, beech and sugar maple from the mixed mesophytic association to the south assumed dominance, and gave rise to the beech-maple association. It is undergoing change in its southern part, and is extending northward into the hemlock-white pine-northern hardwoods forest. In southern New England, migration took place along the then emergent continental shelf; a northern lobe of the oak-chestnut forest became established, locally modified by the inclusion of beech and a number of other mesophytes. The nearness of Pleistocene refugia (in eastern Pennsylvania and southern New Jersey, the latter indicated by bog records) and the early migration route (emergent continental shelf), together with initially varied topography (in contrast to the till plains) have combined to bring about a forest vegetation much like that to the south of the glacial boundary. Near the northwestern corner of the deciduous forest in Wisconsin and Minnesota, early migration took place from the Driftless area and adjacent very old drift areas.<sup>14</sup> That the hemlock-white pine-northern hardwoods forest of the Lake Region did not reach its present position by direct northward migration from the south is indicated by pollen spectra. Farther east, in the high plateau of northern Pennsylvania, this forest climax still persists on unglaciated land, and there is evidence that this area (or somewhat southward of it) was a migratory center.

#### SUMMARY

It is apparent from this chronological picture of events that the several forest regions have had more or less distinct histories involving differences in uplift or submergence, in the number of erosion cycles and extent of peneplanation, in glaciation or the influence of glaciation. The vegetation of these regions reflects these past influences. Most important of these are the development of the Schooley peneplain, and later, of the Harrisburg peneplain (and its

correlatives), the gradual emergence of the Coastal Plain and its Pleistocene submergences, and, in the north, the advance of the great continental glaciers. Changes of temperature are expressed in latitudinal shifts of vegetation in the Tertiary and in glaciation in the Quaternary; of precipitation (or the rainfall-evaporation ratio) in the west-to-east movements most apparent in late Tertiary and in post-glacial time.

Migrations of forest genera, incompletely recorded in the fossil record, point to a gradual separation into what we now think of as northern and southern forms. Latitudinal zonation was apparent even in the early Tertiary. The combinations of genera of the early and middle Tertiary, however, do not suggest a segregation of types related to unlike moisture climates; a mixed forest is indicated. Migrations of forest genera, and of forest communities are suggested by the present distribution of species and communities in relation to the age and history of the land area which they occupy.

As a result of these far-reaching physiographic and climatic influences, the deciduous forest as we know it gradually developed; the major forest associations have arisen, and the present pattern of forest distribution has resulted.

The mixed mesophytic association is the lineal descendant of the mixed forest of the Tertiary, persisting where the Schooley peneplain has never been destroyed by the development of a later peneplain, particularly in those parts of the ancient Schooley peneplain area where that peneplain was never perfected. The mixed mesophytic association is extending its area, as indicated by isolated occurrences (advance disjuncts) on dissected areas within the glacial margin, on slopes of the present erosion cycle in the Great Valley, Piedmont Plateau, and Coastal Plain.

From the mixed forest of the Tertiary, or from its Quaternary representative, the other associations of the deciduous forest have arisen.

The oak-hickory association developed as a result of increasing aridity in Pliocene time, which eliminated the more mesophytic genera from what is now the interior grassland of the United States, and from much of the area west of the Appalachian Plateau.

A late Tertiary origin of the white oak and oak-hickory forests of the Great Valley and Piedmont Plateau is suggested by their correlation with the Harrisburg peneplain.

The oak-chestnut association is another result of the Harrisburg cycle of erosion.

The beech-maple association arose as a result of postglacial migrations from the mixed mesophytic association. It is a young association, whose southern boundary is correlated with an age boundary—the limits of Wisconsin glaciation.

The maple-basswood forest is also young, and at least in part postglacial in origin. It seems to have

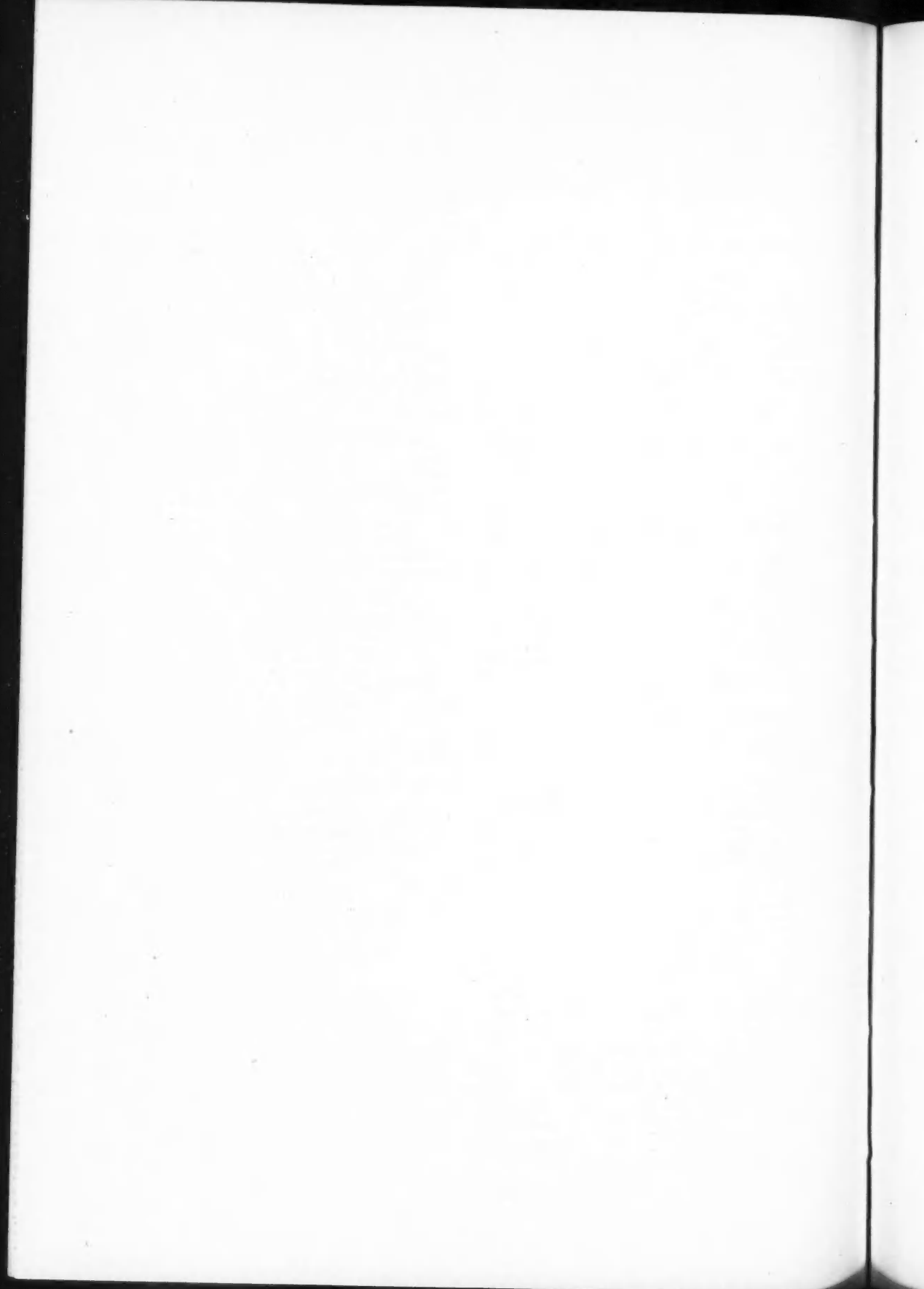
<sup>14</sup> This is indicated by the pollen records and by the nature of present vegetation.

been derived by migrations from a Pleistocene refugium in and near the Driftless area.

The hemlock-white pine-northern hardwoods forest spread from its Pleistocene center in unglaciated northern Pennsylvania.

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SOME NATURAL FLORISTIC AREAS IN BOREAL AMERICA

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IN A SYMPOSIUM ON  
ORIGIN AND DEVELOPMENT OF NATURAL FLORISTIC AREAS WITH  
SPECIAL REFERENCE TO NORTH AMERICA

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# SOME NATURAL FLORISTIC AREAS IN BOREAL AMERICA

## INTRODUCTION

A comprehensive discussion of natural phytogeographic areas in boreal America, even if I were able to produce it, would not be compressible into the time allotted for my contribution to this symposium. I have, therefore, chosen to outline a single problem which has led me into a study of some boreal plant ranges. These ranges, when they are superposed and sorted into patterns, supply evidence of natural floristic areas, and afford some implications of the history and manner of development of these areas.

I have had occasion, during the past few years, to study the vegetation of the southwestern part of the District of Mackenzie, in northwestern Canada. Included in this area are the eastern slopes of the Mackenzie Mountains, a range extending in a great arc northwestward from the Liard River into central Yukon (Fig. 1). The highest altitudes attained in these mountains are as yet unknown, but peaks 7,000-9,000 feet above sea-level are not uncommon. Timber line in the southern part of the range is at about 4,500 feet, but is somewhat lower at the north. The range as a whole is separated from the Rockies, Cascades, Coast Ranges and Richardson Mountains by forested valleys and plateaus.

The flora of the Mackenzie Mountains is still very incompletely known. Prior to our own collections only a handful of plants had ever been gathered there. In 1939 we spent two months at Glacier or Brintnell Lake, in the central part of the range, and in 1944 the route of the Canol pipeline road was examined by Mr. A. E. Porsild who made extensive collections (Porsild 1945). Also in 1944 Dr. V. C. Wynn-Edwards made some notable collections in the eastern fringes of the mountains, and also along the eastern part of the pipeline road. The only place, however, in which anything like a comprehensive collection has been made on the eastern side of the mountains is at Brintnell Lake. The vascular flora of this area proved to be comparatively small—283 species and varieties—with a certain amount of rather poorly defined endemism.

## GEOGRAPHIC AFFINITIES OF THE BRINTNELL LAKE FLORA

### PRELIMINARY REMARKS, INCLUDING NOTES ON LOCAL AND COSMOPOLITAN SPECIES

In order to study the geographic affinities of the Brintnell Lake flora I have mapped the ranges, in Alaska, Canada and the northern States, of 271 of the 283 species and varieties collected there.<sup>1</sup>

When the maps are superposed it becomes possible to designate a number of rather well-defined patterns.

<sup>1</sup> The base map used for these ranges is by J. Paul Goode, and is copyrighted and published by the University of Chicago Press.

The actual number of these patterns depends of course upon the degree of refinement that enters into the selection of criteria. Needless to say, the scanty existing knowledge of geographic factors in boreal America makes it impossible to carry the refinement very far. Comparison of the maps soon brings out, however, two phytogeographic transition zones which appear to overshadow any others that appear. These are the arctic timber line, and the coastal mountains of southeastern Alaska, British Columbia, and western Washington. Some indication of the significance of these "boundaries" may be had from the following figures. Of the 271 species considered in the maps 199 approach or cross the arctic timber line, and 164 of them are either stopped by it or cross it to a limited distance. Nearly all 283 of the Brintnell Lake plants extend to the western coastal mountains or forests, but about 196 of them avoid all or part of these habitats. In view of the obvious phytogeographic importance of the coast range and the arctic timber line, I have drawn up a tentative classification of range patterns based in large part upon the plants' behavior with relation to them. A third geographic boundary is not so well defined in all cases, but is sufficiently clear to necessitate recognition. This is marked by the eastern ranges of the Cordillera. About 25 percent of the Brintnell Lake flora does not extend east of the Rocky Mountains, or has limited extensions into the northern great plain of the continent.

About 4.2 percent of the flora at Brintnell Lake (12 spp. and vars.) is composed of plants recently described as new, recently described from the lower Mackenzie district, or known in North America from this single area (Raup 1947). Tentative ranges can be drawn for a few of these, but so little has been discovered about them that I have preferred to keep them in a separate category, and I have not included maps of them. They are as follows:

*Picea glauca* var. *Porsildii* Raup, *Poa Brintnellii* Raup, *Carex Soperi* Raup, *Salix Barrattiana* var. *marcescens* Raup, *Salix Bebbiana* var. *depilis* Raup, *Salix glauca* var. *perstipula* Raup, *Lychnis brachycalyx* Raup, *Saxifraga sibirica* L., *Rosa acicularis* var. *cucurbitiformis* Raup, *Arnica alpina* (L.) Olin, *Arnica Snyderi* Raup, *Antennaria* sp.

At the other extreme in range extension are three cosmopolitan species: *Cystopteris fragilis*, *Equisetum arvense*, and *Carex aquatilis* s. l. These are among the most wide-ranging plants in boreal America, and the first two are cosmopolitan throughout much of the world. In Canada and Alaska they thrive in nearly all parts of the arctic, alpine, and forest regions, without regard to boundaries that are limiting to most other plants. Of the three, *Equisetum arvense* seems to have the most varied stations.

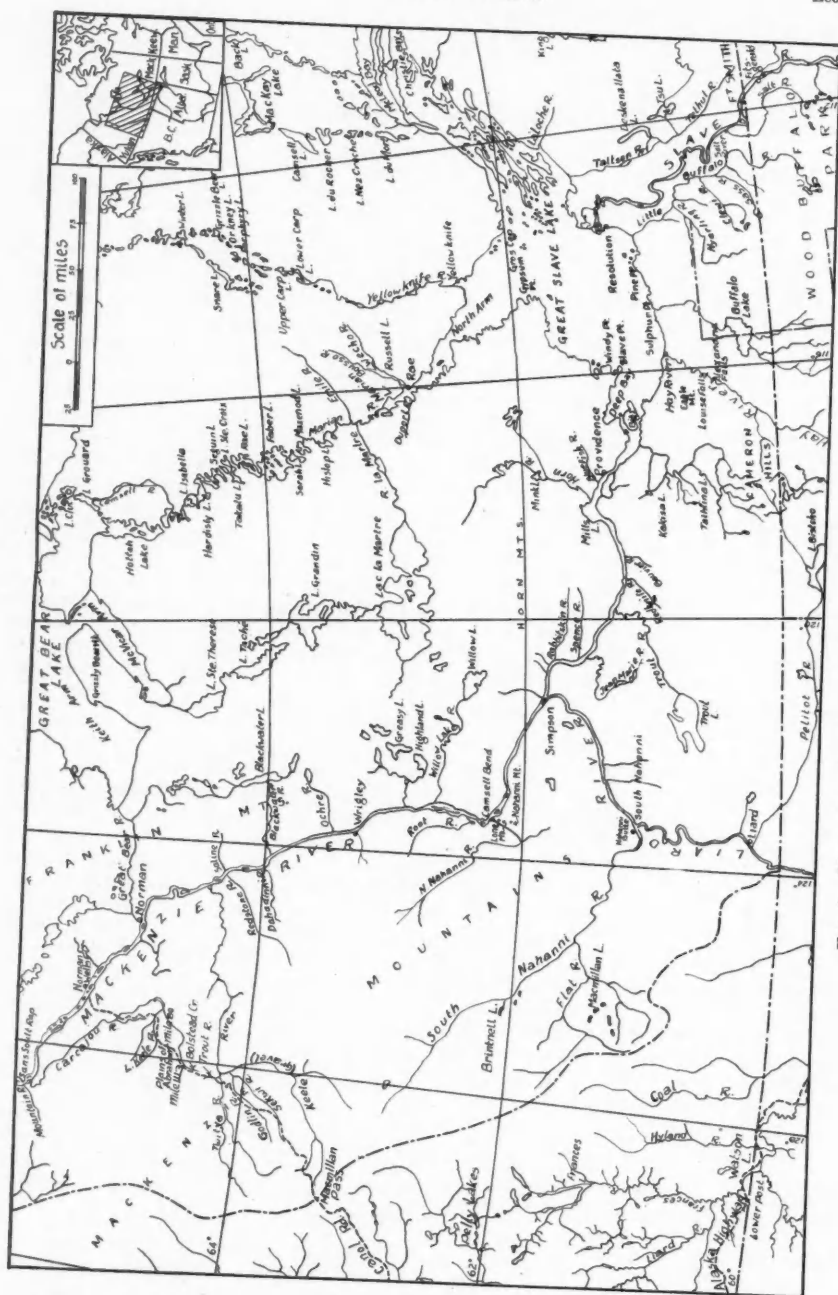


FIG. 1. Map of southwestern Mackenzie and adjacent regions.

The remaining 268 species and varieties can be arranged in five general categories: (1) species whose principal areas are in the region of the Canadian coniferous forest, and whose ranges are wide in this region, extending for the most part all the way across the continent; (2) arctic or arctic-alpine wide-ranging species with ranges concentrated north of the arctic

timber line, or in both the arctic lowland and in the cordilleran alpine areas; (3) an intermediate group of wide-ranging subarctic species which cannot be placed with either of the above, but which appear to have their greatest concentration on or near the arctic timber line; (4) a group of Alaskan-cordilleran species which have only limited extensions east of the

Rocky and Mackenzie Mountains, and most of which are arctic-alpine in general affinities; (5) a cordilleran group, most of which are alpine but not arctic, and whose ranges are concentrated in the Rocky Mountains and coast ranges. Further subdivisions of these five categories can be made by noting first the actual relation of the wider ranges to the arctic timber line, and second the relation of the ranges to the western coastal mountains or the Pacific slope forests. The following discussion will follow the above outline.

In order to compare the range maps more easily I have drawn lines connecting marginal stations in such a way as to outline the limits to which the various species are now known to extend. For common, much collected plants this can be done without difficulty, but in cases of rare or poorly collected species the outlines of geographic limits must be regarded as tentative. The most difficult cases are those with stations separated by hundreds of miles. Here it is often impossible to decide whether to consider the ranges as continuous or disjunct. Of the ranges mapped in this study I have designated only nine as being discontinuous, although it is possible that a few others might be included. In defense of my tendency to reduce the number of disjunct ranges as much as possible I can only say that one of the results of the collecting and exploration in arctic and subarctic America during the past twenty years has been to fill in and make continuous many ranges that were formerly thought to have separate eastern and western components.

#### WIDE-RANGING FOREST SPECIES

The most extensive plant ranges in Canada and Alaska, with the exception of the three cosmopolitans already mentioned, are exhibited by a small group of about 19 species. These plants do not stop at the arctic timber line, but reach far out into the tundra, particularly in the eastern arctic. Most of them are spread throughout the timbered parts of Alaska. Eight of them (Fig. 2A) have the widest ranges because they also enter the forests of the Pacific slope from southern Alaska to western Washington:

*Equisetum scirpoides*, *Poa pratensis* s. l., *Corallorrhiza trifida*, *Alnus crispa* s. l., *Rubus Chamaemorus*, *Epilobium angustifolium* s. l., *Pyrola secunda*, *Ledum groenlandicum*.

The other 11 species either avoid the coastal forests altogether, or enter them only in southern Alaska or Washington. Thus they are more strictly continental in the far west (Fig. 2B):

*Calamagrostis neglecta*, *Carex vaginata*, *Habenaria obtusata*, *Salix planifolia*, *Betula glandulosa*, *Ranunculus Gmelini* var. *Purshii*, *Ranunculus lapponicus*, *Draba lanceolata*, *Potentilla fruticosa*, *Hedysarum alpinum* var. *americanum*, *Vaccinium Vitis-Idaea* var. *minus*.

The remainder of the widespread forest species are more rigorously limited by the timber line, though some of them occur far north on the Labrador coasts, southern Baffin Island, or in Greenland. There are 80 of them, divisible into four groups on the basis of their geographic relation to the Pacific slope forests. The first of these groups (Fig. 3A) contains 30 species that appear in the coastal forests both in southern Alaska and in British Columbia and western Washington. Several of them, perhaps half a dozen, do not appear to reach the western coast of Alaska.

*Dryopteris Linnacana*, *Equisetum fluviatile*, *Equisetum palustre*, *Lycopodium annotinum* s. l., *Selaginella selaginoides*, *Juniperus communis* var. *montana*, *Agrostis scabra*, *Poa nemoralis*, *Carex leptalea*, *Carex canescens*, *Carex Gorberi* s. l., *Juncus balticus* s. l., *Smilacina stellata*, *Habenaria hyperborea*, *Salix Bebbiana*, *Arenaria lateriflora*, *Stellaria calycantha* s. l., *Actaea rubra*, *Ribes lacustre*, *Ribes triste*, *Shepherdia canadensis*, *Cornus canadensis*, *Cornus stolonifera*, *Moneses uniflora*, *Pyrola asarifolia* var. *incarnata*, *Pyrola minor*, *Heracleum lanatum*, *Arctostaphylos Uva-ursi* (incl. var. *coactilis*), *Linnaea borealis* s. l., *Viburnum edule*.

The second group, of 13 species (Fig. 3B), occurs in some of the coastal forests of southeastern Alaska, but becomes more continental in British Columbia and Washington. A few of them, probably not more than four, fail to reach the western Alaskan Coast.

*Equisetum sylvaticum* s. l., *Lycopodium clavatum* var. *monostachyon*, *Lycopodium complanatum* s. l., *Carex gynocrates*, *Eriophorum brachyantherum*, *Cypripedium passerinum*, *Populus Tacamahacca*, *Populus tremuloides*, *Geocaulon lividum*, *Parnassia palustris* var. *neogaea*, *Ribes hudsonianum*, *Dryas Drummondii*, *Rosa acicularis* s. l.

A third group of 14 species (Fig. 3C) is still more continental in range, reaching the coast timber only in southwestern British Columbia and western Washington. They avoid the wet slope forests of southern

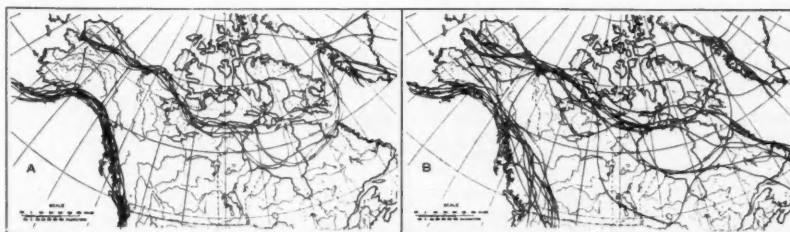


FIG. 2. Wide-ranging forest species extending north of the arctic timber line.

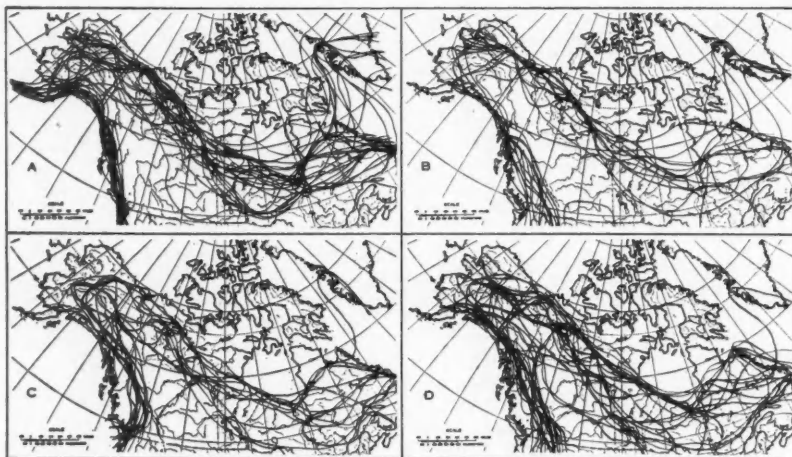


FIG. 3. Wide-ranging forest species whose northern limits are at or near the arctic timber line.

Alaska, and none of them extends to the western coasts of Alaska. Four of these plants seem to have disjunct ranges: *Arctostaphylos Uva-ursi* var. *adenotricha*, *Betula papyrifera* var. *commutata*, *Arabis Holboellii*, *Antennaria subviscosa*. I have included them here because a hypothetical joining of their parts would result in ranges similar to the others in Fig. 3C.

*Carex aurea*, *Betula papyrifera* var. *commutata*, *Arenaria dawsonensis*, *Arabis Drummondii* s. l., *Arabis Holboellii*, *Geum macrophyllum* var. *perincisum*, *Potentilla norvegica*, *Pyrola virens*, *Arctostaphylos Uva-ursi* var. *adenotricha*, *Erigeron angulosus* var. *kamtschaticus*, *Erigeron elatus*, *Antennaria subviscosa*, *Senecio indecorus*, *Senecio pauperculus*.

The fourth, and almost strictly continental, group contains 23 species (Fig. 3D). With one or two possible exceptions these plants avoid the Pacific slope forests entirely, and all but five of them fail to reach the west coasts of Alaska. A few are even more restricted and do not extend west of the northern Rocky Mountains.

*Picea glauca* s. l., *Picea mariana*, *Agropyron trachycaulum* var. *novae-angliae*, *Agropyron trachycaulum* var. *unilaterale*, *Calamagrostis canadensis* var. *robusta*, *Carex concinna*, *Carex diandra*, *Carex media*, *Goodyera repens* s. l., *Listera borealis*, *Salix myrtillofolia*, *Alnus tenuifolia*, *Betula occidentalis*, *Aquilegia brevistyla*, *Rorippa islandica* var. *microcarpa*, *Ribes glandulosum*, *Ribes oxycanthoides*, *Amelanchier florida* (incl. *A. humilis*), *Fragaria glauca*, *Rubus acaulis*, *Rubus strigosus*, *Mertensia paniculata*, *Valeriana septentrionalis*.

#### WIDE-RANGING ARCTIC-ALPINE PLANTS

There are 66 wide-ranging arctic-alpine plants in the Brintnell Lake flora. As among the forest species, one can first divide them into two groups according to their actual relation to the arctic timber line. In spite of the fact that the principal ranges of nearly all of them extend throughout much of the

arctic archipelago, 26 of them are commonly found far south of the arctic limit of trees (Fig. 4). In so doing they achieve the most extensive ranges of all our arctic-alpine plants and, as did the forest species that crossed the timber line, they approach a cosmopolitan distribution in Canada and Alaska.

The most extensive ranges are those of 7 species (Fig. 4A) which occur not only on the Rocky and Mackenzie Mountains but also on the coastal ranges all the way from the Alaska Peninsula to Washington. They extend southward in the central plains at least as far as Lake Athabaska.

*Equisetum variegatum*, *Lycopodium Selago*, *Festuca brachyphylla*, *Poa alpina* s. l., *Carex scirpoidea*, *Salix arctica* s. l., *Empetrum nigrum*.

Another group, of 8 species, is predominantly continental south of the mountains in southeastern Alaska (Fig. 4B). They occur on the coast and Alaska ranges of southern Yukon and Alaska, as well as on the mountains around the Lynn Canal, but in British Columbia and Alberta they are largely confined to the Rockies and Selkirks.

*Poa glauca*, *Trisetum spicatum* s. l., *Carex capillaris* s. l., *Juncus castaneus*, *Polygonum viviparum*, *Saxifraga tricuspidata*, *Dryas integrifolia*, *Astragalus alpinus*.

A third group of these extremely wide-ranging arctic-alpine plants contains 11 species (Fig. 4C) and is almost completely continental in the west. Southeast of the Prince William Sound region of Alaska these plants are confined to the more northerly ranges of the coastal mountains, and to the Rockies and Selkirks. Only two of them come out to the coast in northwestern Washington.

*Dryopteris fragrans* s. str., *Calamagrostis purpurascens*, *Arenaria verna* var. *pubescens*, *Ranunculus hyperboreus*, *Cardamine pratensis* s. l., *Draba cinerea*, *Chrysosplenium tetrandrum*, *Saxifraga aizoides*, *Potentilla nivea* s. l., *Pyrola grandiflora* s. l., *Taraxacum lacerum*.

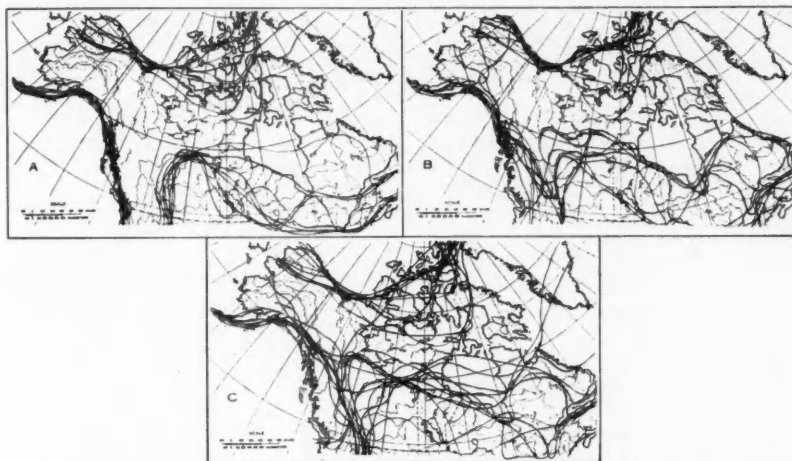


FIG. 4. Wide-ranging arctic and arctic-alpine species which extend far south of the arctic timber line.

For the remaining 40 arctic-alpine plants the arctic timber line appears to be a more formidable barrier. They either stop at the timber line or come only a short distance south of it. Like the preceding group they can be arranged in three divisions depending upon whether they extend to the mountains of the Pacific coast.

First are 12 species of wide range on the coastal mountains (Fig. 5A). One of these, *Dryas octopetala*, has a broken range. It is widespread in the Cordillera and reappears in northwestern Greenland.

*Agropyron latiglume*, *Poa arctica*, *Luzula spicata*, *Oxyria digyna*, *Silene acaulis* var. *exscapa*, *Cardamine bellidifolia*, *Saxifraga oppositifolia*, *Saxifraga rivularis*, *Dryas octopetala*, *Epilobium latifolium*, *Epilobium anagallidifolium*, *Erigeron unalaschkensis*.

Another group of 10 species ranges the coastal mountains only in southern and southeastern Alaska (Fig. 5B). In British Columbia and Alberta they reach their southern limits in the Rockies and Selkirks, and are strictly continental.

*Hierochloë alpina*, *Carex bipartita*, *Eriophorum Scheuchzeri*, *Luzula Wahlenbergii*, *Salix reticulata*, *Salix Richardsonii*, *Oxytropis foliolosa*, *Cassiope tetragona*, *Pedicularis capitata*, *Pedicularis sudetica*.

Finally, a group of 18 arctic-alpine plants, with one exception in western Washington, avoid the coastal mountains entirely (Fig. 5C).

*Calamagrostis lapponica* s. l., *Carex membranacea*, *Luzula confusa*, *Arenaria humifusa*, *Arenaria Rossii*, *Lynchnis apetal*, *Stellaria longipes* var. *Edwardsii*, *Ranuncu-*

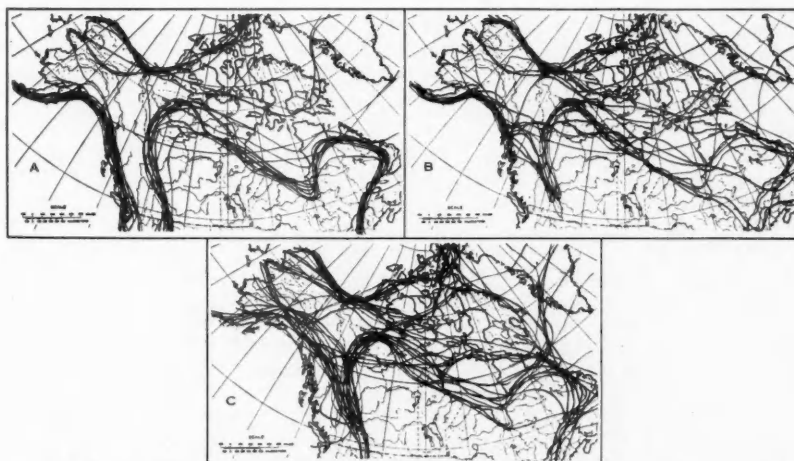


FIG. 5. Wide-ranging arctic and arctic-alpine species whose southern limits are at or near the arctic timber line.



*lus nivalis*, *Draba fladnizensis* var. *heterotricha*, *Draba glabella*, *Saxifraga nivalis*, *Potentilla emarginata*, *Oxytropis Maydelliana*, *Epilobium davuricum*, *Vaccinium uliginosum* var. *alpinum*, *Pedicularis lanata*, *Erigeron eriocephalus*, *Crepis nana*.

Two features of the arctic-alpine plant ranges should be noted especially. Nearly all of them extend to the western Alaskan coasts, in contrast to the forest plants among which 39 do not accomplish this. Second, there are a few of the arctic plants, probably not more than 8, which do not occur in the Rocky Mountains at all, but find their southern limits in the Mackenzie Mountains and in southern Yukon or Alaska.

#### PLANTS OF THE TIMBER LINE REGION

There are 31 species which constitute something of an enigma in that, although they have wide subarctic ranges across most of the continent, they cannot properly be classed either with forest or arctic-alpine categories. They extend into the tundra, but avoid most of the high arctic regions. At the same time they are common to abundant in the northern part of the forest. They occupy a wide range of habitats, although none of them is characteristic of rich woods, and about two-thirds of them are perhaps most abundant in muskogs or wet tundra. Most of them appear in the northern Rockies, but two or three do not come south of the 60th parallel. All but two or three reach the western Alaskan coasts.

A glance at Fig. 6 will show that most of these "timber line" species are continental in the more southern parts of their ranges. I have arranged them in two groups, carrying out the plan used in other categories. The first group contains 10 species which occur in the coastal strip as far south as southeastern Alaska, while beyond that area all but 3 retreat inland (Fig. 6A). One species of disjunct range is included here, *Lycopodium alpinum*.

*Woodsia ilvensis*, *Lycopodium alpinum*, *Calamagrostis canadensis* var. *Langsdorffii*, *Cerastium Beeringianum*, *Anemone parviflora*, *Anemone Richardsonii*, *Sibbaldia procumbens*, *Andromeda Polifolia*, *Vaccinium microcarpum*, *Vaccinium uliginosum*.

A second group, of 21 species, avoids the coastal strip except in southwestern British Columbia, where four of them come out to Vancouver Island (Fig. 6B). Three species with discontinuous ranges are in this group: *Sagina Linnaei*, *Epilobium lactiflorum*, *Oxytropis izodes*.

*Carex deflexa*, *Carex microglochin*, *Tofieldia palustris*, *Salix glauca* s. l., *Arenaria sajanensis*, *Sagina Linnaei*, *Parnassia Kotzebuei*, *Hedysarum Mackenzii*, *Oxytropis hudsonica*, *Oxytropis izodes*, *Epilobium lactiflorum*, *Cornus canadensis* f. *purpurascens*, *Arctostaphylos rubra*, *Gentiana propinqua*, *Pedicularis labradorica*, *Veronica alpina* var. *unalaschensis*, *Pinguicula villosa*, *Solidago multiradiata*, *Antennaria isolepis*, *Taraxacum ceratophorum*, *Taraxacum lapponicum*.

#### ALASKAN-CORDILLERAN SPECIES

An arrangement of Alaskan and cordilleran components of the Brintnell Lake flora on the basis of their relation to timber line proves to be impracticable. Of the 72 species counted in these categories, only ten can be regarded as forest plants, and most of these ten are likely to be found far above or beyond the timber line. All the others are plants commonly found in the alpine or western arctic tundra. However, a great many alpine plants of the Mackenzie and northern Rocky Mountains are commonly found in the timbered areas at low levels. About half of the western alpine plants were found below timber line at Brintnell Lake, and no doubt further search would yield more of them. It is not possible, therefore, safely to classify them in relation to timber line.

I have arranged the 72 species in two main groups, the first of which ranges throughout central and western Alaska, many of them north to the arctic coast. Most of them come into the mountains farther south, so that I have called them the Alaskan-cordilleran group. There are 45 of these, 16 of which (Fig. 7A, C) range southward into the western United States. The whole group can be separated on the basis of its coastal extensions. First is a wide-ranging series of 11 species, all of which occur on the coastal mountains of southeastern Alaska, and many of them on the coast ranges farther south (Fig. 7A).

*Carex physocarpa*, *Luzula arcuata*, *Lloydia serotina*, *Zygadenus elegans*, *Arabis lyrata* var. *kamchatica*, *Sedum roseum* var. *integrifolium*, *Viola epipsila*, *Gentiana glauca*, *Aster sibiricus*, *Artemisia arctica* s. l., *Petasites frigidus*.

Allied to these, but with their southern extensions terminating in Yukon or the Alberta and British Columbia Rockies, are 15 species, all of which are coastal in southern or southeastern Alaska (Fig. 7B).

*Cryptogramma crispa* var. *sitchensis*, *Arctagrostis arundinacea*, *Festuca altaica*, *Poa paucispicula*, *Carex liliacea*,

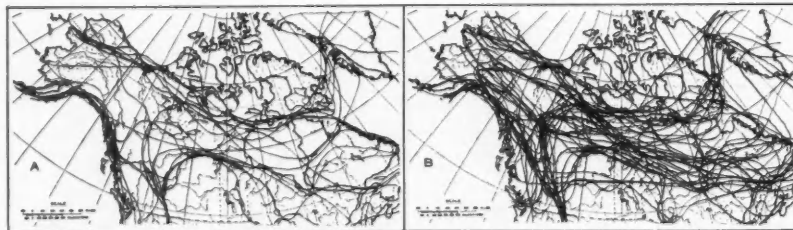


FIG. 6. "Timber-line species."

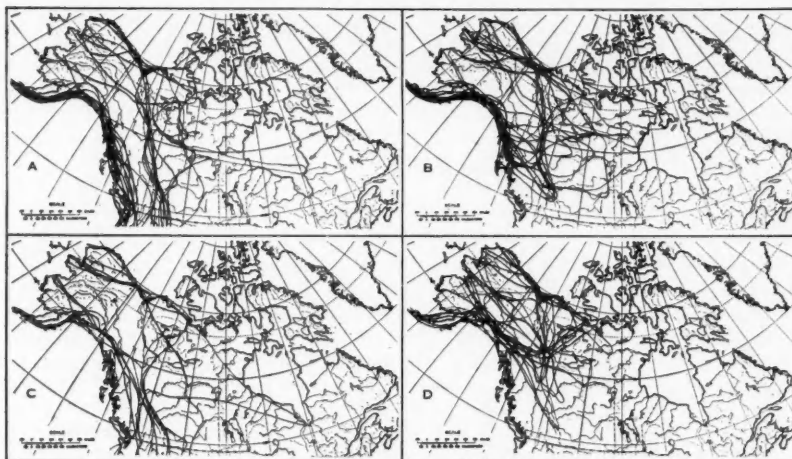


FIG. 7. Alaskan-cordilleran species.

*Salix alaxensis* s. l., *Salix arbusculoides*, *Salix pulchra*, *Betula papyrifera* var. *humilis*, *Aconitum delphinifolium*, *Anemone narcissiflora*, *Saxifraga punctata* s. l., *Boschniakia rossica*, *Campanula lasiocarpa*, *Arnica Lessingii*.

Two groups are more strictly continental in the region southeast of Prince William Sound, although a couple of species appear at the coast in the Puget Sound area. Five species range southward into the United States (Fig. 7C).

*Delphinium glaucum*, *Potentilla uniflora*, *Myosotis alpestris* s. l., *Artemisia Tilesii* s. l., *Senecio lugens*.

The remainder, 14 species, extend from Alaska to the northern Rocky Mountains, and avoid the coastal mountains except west of Prince William Sound (Fig. 7D).

*Larix laricina* var. *alaskensis*, *Carex nesophila*, *Carex podocarpa*, *Corydalis pauciflora*, *Draba longipes*, *Saxifraga radiata*, *Astragalus frigidus* var. *littoralis*, *Lupinus arcticus*, *Oxytropis hyperborea*, *Oxytropis pygmaea*, *Gentiana aretophila*, *Polemonium acutiflorum*, *Antennaria monocephala*, *Taraxacum alaskanum*.

#### CORDILLERAN SPECIES

The last category of ranges to be considered involves 27 plants that are more strictly cordilleran than any of the above. They do not reach the arctic

coast proper, either in Alaska or Mackenzie, and their eastward extensions into the northern plains are less numerous and less pronounced. All of them range southward into the western United States. They fall rather clearly into two groups: one with a strong coastal relationship and the other just as strongly continental.

Sixteen of the 27 follow the coastal mountains from the Alaska Peninsula to western Washington, although a couple of them retreat inland a short distance in the latter region. They extend throughout the northern Rocky Mountains, but most of them are confined to the southern ranges of Alaska. None of them reaches the lower Yukon valley (Fig. 8A), although two have been found at the Mackenzie River delta. Our Mackenzie Mountain collections have constituted northeastern range extensions for most of these species.

*Abies lasiocarpa*, *Carex nardina* var. *Hepburnii*, *Carex phacocephala*, *Carex pyrenaica*, *Juncus Drummondii*, *Salix Barclayi*, *Salix commutata*, *Salix Scouleriana* s. l., *Ranunculus Eschscholtzii*, *Draba nivalis* var. *elongata*, *Parnassia fimbriata*, *Saxifraga Lyallii*, *Hippuris montana*, *Phyllodoce glanduliflora*, *Senecio triangularis*, *Hieracium gracile*.

The other 11 cordilleran plants avoid the coastal strip except in the south, where four of them appear

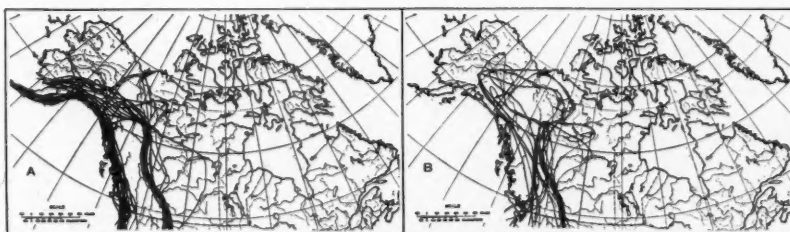


FIG. 8. Cordilleran species.

in the Puget Sound region. A few of them (4) reach central Alaska, and two are found at the Mackenzie delta (Fig. 8B). This group contains the very few Rocky Mountain plants which have their known northern limits in the Mackenzie Mountains.

*Poa Buckleyana*, *Carex albonigra*, *Carex atrata* ssp. *atroscama*, *Salix Barrattiana*, *Draba McCallae*, *Draba praealta*, *Potentilla diversifolia* s. l., *Erigeron jucundus*, *Antennaria media*, *Arnica mollis*, *Arnica alpina* ssp. *toментosa*.

#### DISCUSSION

Table 1 gives a summary of the range patterns just described. Some generalizations from these figures will serve to bring out further the regional characteristics and affinities of the Brintnell Lake Flora. Fully 70 percent or about 199 of the species, have wide ranges across the continent, most of them extending from Alaska to the Gulf of St. Lawrence. Approximately 25.4 percent are Alaskan or cordilleran, while the remaining 4.2 percent are endemic or local.

TABLE 1

	No. of sp. and vars.	Percent
Endemics and plants of limited known range	12	4.2
Cosmopolitan in Canada and Alaska	3	1.0
Wide-ranging forest species		
Reaching coasts of Alaska, B.C., and western Washington	38	13.4
Reaching coasts of southeastern Alaska	13	4.6
Avoiding coasts, southeastern Alaska to Washington	48	17.0
Wide-ranging arctic or arctic-alpine species		
Reaching coastal mountains, Alaska to Washington	19	6.7
Reaching coastal mountains of southeastern Alaska	18	6.4
Avoiding coastal mountains, S.E. Alaska to Washington	29	10.2
Wide-ranging "timber-line" species		
Reaching coast of S.E. Alaska	10	3.5
Avoiding coasts, S.E. Alaska to Washington	21	7.4
Alaskan-cordilleran species		
Reaching coasts, Alaska to Washington	11	3.9
Reaching coasts of southern and southeastern Alaska	15	5.3
Avoiding coasts, S.E. Alaska to Washington	19	6.7
Cordilleran species		
Reaching coasts, southern Alaska to Washington	16	5.6
Avoiding coasts, southern Alaska to Washington	11	3.9
TOTALS	283	99.8

The wide-ranging plants fall into two main groups, arctic-alpine and forest species. In the first there are 66 species, while in the second there are 99. A third group of 31 species (10.9 percent) are intermediate between the first two, and three (1 percent) are cosmopolitan. This is not a complete statement of the proportions of arctic-alpine and forest elements, however, because approximately 62 of the 72 Alaskan and cordilleran plants are of prevalently alpine or arctic affinity and should be added to the wide-ranging ones. Thus the total of arctic, arctic-

alpine, and alpine plants is about 128, or about 45 percent of the total vascular flora, and that of forest species is 109, or about 38 percent of the whole.

Although the flora as a whole is strongly continental in character, a great many of its species are able to live in the damp forests of the north Pacific slopes or on the coastal mountains. The range maps give a rough index to the degree of continentality which is achieved by the Brintnell Lake flora. There are about 140 species (49.4 percent) which avoid the coastal forests and mountains completely or nearly so, and are the most rigorously continental plants in our flora so far as the west is concerned. Another 56 (19.8 percent) avoid the British Columbia and Washington coasts, but occur in southeastern Alaska. The remaining 87 (30.7 percent) inhabit, in addition to the continental ranges, the coastal strip from Alaska to Washington.

Table 2 will summarize the above generalizations.

TABLE 2

	No. of sp. and vars.	Percent
Endemics and plants of limited known range	12	4.2
Cosmopolitan species	3	1.0
Plants of wide range across the continent	199	70.3
Plants with ranges mainly in Alaska and the Cordillera	72	25.4
Plants of the forested country	109	38.0
Arctic, arctic-alpine, or alpine species	128	45.0
"Timber-line" ranges	31	10.9
Strictly continental with regard to S.E. Alaska, B. C., and Washington	140	49.4
Plants that avoid the coasts of B. C. and Washington, but occur in S. E. Alaska	56	19.8
Plants whose ranges extend into the coastal strip of S.E. Alaska, B. C., and Washington	87	30.7
Plants that do not reach the western coasts of Alaska	81	30.0

#### APPLICATION OF HULTÉN'S HYPOTHESIS

In view of the geographic position of the Mackenzie Mountains in northwestern America, their recent botanical exploration, the present isolation of their alpine flora by the development of surrounding forests, and the simplicity and apparently incipient endemism in their flora, it has occurred to me that this flora might be used as a test of theories advanced some years ago (1937) by Dr. Eric Hultén concerning the origin and development of all our boreal biota.

Whether or not there were ice-free land surfaces in the Mackenzie Mountains during the Late Wisconsin (W<sub>3</sub>) glacial episode is not certain, although there is some evidence, both geological and botanical, that suggests them. If ice-free summits were present, their flora must have been composed of the arctic-alpine remnants of a wide pre-Late Wisconsin dispersal of these plants. A few species found at Brintnell Lake suggest this. There are three that

have extensive ranges in Eurasia but are not known elsewhere in North America, and there are eight rather poorly defined endemics or suspected endemics. Considering the small number of these unique plants, and the paucity of the Brintnell Lake flora as a whole, it is hardly justifiable to set up the Mackenzie Mountain area, at least so far as the eastern slopes are concerned, as a refuge equivalent to those of Beringia, the North Pacific coasts, or the Yukon Plateau. It seems more reasonable to assume that although a few alpine plants may have persisted at Brintnell Lake through Late Wisconsin time, most of the flora has arrived during and since the retreat of the last valley glaciers. The findings of Porsild on the western slopes of the mountains may require modification of this view.

It is unnecessary to review in detail all of the reasoning and implications of the theories advanced by Hultén, for this has already been done by several students (see Stebbins 1942, Raup 1941, Halliday and Brown 1943, Cain 1944). The following is a brief outline of the broader geographic aspects, with a few critical notes that have grown out of the present investigation.

In connection with his floristic studies of Kamchatka and the Aleutian Islands, Hultén mapped, sometimes in detail and sometimes by limits, the ranges of hundreds of arctic and boreal species. He organized this factual material on the basis of what he called "equiformal areas." That is, when large numbers of ranges are superposed they fall into a group of patterns which are more or less clearly defined geographically, and "equiformal" within themselves. Each equiformal area shows a region of concentration in number of species, which is called its "centre." Since it is assumed that each species has acquired its present range by dispersal from a point of origin or survival, the regions of concentration within the equiformal areas are regarded as fundamental centers of origin for the various major elements in the flora; and the "equiformal areas" become "equiformal progressive areas" that are thought to indicate the general patterns of dispersal among the major elements. The species are termed "radiants" from the various "centra."

The geographic arrangement of centra as worked out by Hultén is as follows: They are "... in North-Eastern Siberia and in the Amur-Manchurian region. Another occurs in the Altai-Sajan region, sending out radiants towards the Arctic shore. A third centre is northern Japan, whence numerous plants radiate to the north and to the coast of the Asiatic Continent. A centre of great importance is the region around the northern part of the Bering Sea. It sends out progressive radiants reaching symmetrically as well to the west into arctic Asia and Europe as to the east to Eastern America, and also often extends arms along both the Asiatic and American Pacific coast. In America radiants proceed from the Yukon valley along the Arctic American coast, others centre around the Arctic Archipelago, and others again have the centre of their progressive figures in the State of

Washington and radiate along the American coast or along the Rocky Mts. to Alaska. Of the plants discussed . . . no groups could be formed having their centres in northern Europe or western Siberia, or in North-Eastern America or in the country between Yukon Valley and the Great Lakes" (Hultén 1937, p. 25).

Hultén immediately draws a correlation between the distribution of his centra and the distribution of ice during the Pleistocene. No centra could be found in areas that were covered by ice during the maximum advance of the glaciers; and the existing floras have all been derived from areas of refuge close to the ice. It is maintained, on genetical grounds, that the ability of the species to disperse themselves from their refugia has not been uniform. Those confined to small refugia, under difficult climatic conditions and in small populations, are considered to have been so depauperated of biotypes that they have been exceedingly slow to spread. Others had large areas and populations, either within the generally glaciated regions or south of the ice, so that they retained their inherent variability and aggressiveness and could quickly invade lands freed of ice.

It is thought that the so-called "Linnaean species" of the present boreal flora originated in the last great interglacial or earlier, and that large numbers of them achieved wide dispersals during that time. Their present areas are looked upon as reductions from these wide ranges, with post-Glacial re-expansions that have been conditioned by the amount of depauperation suffered during the maximum ice advance.

Hultén's arrangement of equiformal areas is open to modification or criticism along three lines. First, it is possible to make additions to his lists, at least in the American boreal flora. The Brintnell Lake region is found to have approximately 45 species not discussed by him at all. When these are sorted into patterns they have a distribution among the equiformal areas, however, that makes no serious modification in the latter. Second, there are apparent gaps in the ranges of boreal American plants which are gaps in exploration rather than in the actual ranges. Lacunae in our knowledge of the more uniform floras of eastern glaciated regions are not so troublesome; but the gaps in northern British Columbia and Yukon are more serious, for the distribution of species into equiformal areas sometimes depends upon their behavior in this region. Some of Hultén's dispositions of species are therefore open to modification due to range extensions discovered since his study was made. Third, Hultén's original sorting of species among his equiformal areas can be questioned in many cases. This is particularly notable in his treatment of wide-ranging forms.

I have found it necessary to make a number of changes in Hultén's lists along the three lines just mentioned. The changes are in many cases matters of judgment, and even when all are taken together they make no serious modification in his general sorting of ranges.

If the general thesis outlined by Hultén is tenable,



then the flora of the Mackenzie Mountains should show affinities with his various centra which, within the general limits of accessibility, are directly proportional to the size of the relic populations, and presumably inversely proportional to their degree of biotype depauperation.

It should be possible to draw up a sequence showing the relative availability of plants for the colonization of the Brintnell Lake area during the retreat of the glaciers. It is presumed that for a time after the disappearance of the ice the mountains and adjacent valleys and plains had free access to the alpine and tundra floras of the Rockies, the Cassiars, the Yukon Plateau, the Richardson Mountains, and the arctic lowlands. With the amelioration of the climate coniferous forests eventually covered the valleys of the Mackenzie, upper Liard, Peel, and Wind Rivers, and finally the divides between these streams and the Yukon system. In so doing they effected the isolation of the alpine and arctic elements of the Mackenzie Mountain flora.

The time intervals are conjectural, but probably can be brought within reasonably definite limits. There is fairly good evidence that forests did not appear in the central Mackenzie basin until after the final retreat of the ice from Great Slave Lake and until after the last of the post-Glacial lakes in the Athabaska-Great Slave Lake region had been drained. Forests probably did not enter southwestern Mackenzie until the period of the climatic optimum, as late as 7,000 years ago. They can hardly have reached the higher, interior valleys and divides until somewhat later.

According to Hultén's theory the first aggressive floristic elements to invade the glaciated lands were the Arctic-Montane plants, and such parts of the Beringian and other groups as are supposed to have reached refugia south of the ice before the maximum advance. In both cases these plants were able to maintain large populations during the last great ice advance, and to maintain their genetic plasticity. The most plastic of all Hultén's groups, and certainly the most wide-ranging species, are among the Boreal Circumpolar plants, but since a very large proportion of this group is of forest species, it cannot be expected to show so high a representation in the Mackenzie Mountains as the arctic-alpine group.

Next to the Arctic-Montane plants in a decreasing scale of availability would come the Continental West American Radiants. These are thought to have survived in the Yukon valley and the northern Rocky Mountains, many of them below the ice boundary. Since they contain a large arctic-alpine element they can be expected to be well represented in the Mackenzie Mountains. Furthermore a part of their refuge areas are directly adjacent to the Mackenzie Mountains.

The various Beringian radiants of Hultén should be rather poorly represented, not only because many of them are thought to have lost their spreading capacity, but also because they, like other alpine elements, were eventually stopped by the advance of the

forests. Another small part of the Mackenzie Mountain flora should be derived from the coastal radiants, for they could not be expected to spread far outside the habitats of the relatively warm and wet north Pacific shores. It is true that Hultén allows many of these coastal species to spread widely across the continent, but they are more southern types that would not be expected at high latitudes.

In Table 3 I have compared Hultén's floristic elements of the Brintnell Lake area in two ways. First the percentages of the total known flora which are derived from the various sources are compared, and second, the percentages of the total numbers of radiants (as revised) from the various sources that are represented in the mountains. Approximately the same results are reached by both methods. The Arctic-Montane group is present in largest numbers. Over 42 percent of all the plants listed in the group have been found at Brintnell Lake, and they make up about 35 percent of the local flora there. Next are the Continental Western American plants, and third, the Boreal Circumpolar group. The Beringian groups, taken together, and the western American Coast Radiants have each supplied only 8.1 percent of the flora. The most strictly coastal group set up by Hultén, of Atlantic-Pacific plants, is not represented at all.

It will be seen at once that these results correlate very well with the series expected on the basis of Hultén's theory. They lend considerable support to his general concept. It should be noted that the results from similar comparisons made with Hultén's unrevised figures are not far different from the above. The positions of the Boreal Circumpolar and Continental West American groups are reversed, but they are not far apart in any case.

Hultén's method of handling his data, however, leaves a great deal to be desired. The success achieved by him probably can be attributed to his perspicacity in "sensing" the geographic relationships of American plants rather than to an objective treatment of his information. This is best shown in his sorting of wide-ranging species into his several groups. It is virtually impossible, for instance, to say whether a wide-ranging arctic-alpine species should be placed among the arctic-montane, boreal circumpolar, or continental western American radiants. The equiformal progressive areas are clear so long as their individual plant ranges are relatively small. The larger ones disappear in the great "pools" of species whose ranges extend all the way across the continent. A few doubtful decisions of this sort would not be serious, but Hultén had to make hundreds of them in order to relate all the ranges to his equiformal areas.

With these difficulties in mind I have tried to sort the actual ranges of the species, so far as they are known, into natural patterns without regard to hypothetical centers of dispersal. Using the maps presented here and the genetic reasoning employed by Hultén, it is possible to arrange a sequence of floristic influences similar to that described above. The size



TABLE 3

	Hultén's totals (amended)	Found at Brintnell Lake	Percentage of total Brintnell L. plants	Percentage of Hultén's amended totals
Local plants, or plants of limited known range.....		12	4.2	
Beringia Radiants.....	248	23	8.1	9.3
Atlantic-Pacific plants.....	16	0	0	0
W. American Coast Radiants.....	267	23	8.1	8.6
Continental W. American Radiants.....	190	73	25.8	38.4
Arctic-Montane plants.....	235	100	35.3	42.6
Boreal Circumpolar plants.....	262	52	18.3	19.9
TOTALS.....	1218	283		

and character of existing ranges can be used as indicators of the success with which plants have migrated from the Pleistocene refugia.

Considering first the alpine flora, by far the largest single group (66 spp.) is derived from wide-ranging arctic-alpine plants—51.5 percent of the alpine, or about 23 percent of the total flora. These are the species that are thought to have maintained comparatively large populations during the Pleistocene, and to have been able to migrate during that time.

Second in extent of range are the species that have occupied wide areas in Alaska or the northern Cordillera or both, some of them extending eastward toward Hudson Bay (maps, Fig. 7A, B, C; Fig. 8). There are 49 of these—about 38.2 percent of the alpine. Finally there are 13 species of far northwestern range (map, Fig. 7D), only a few of which extend south of the 60th parallel. They comprise about 10.1 percent of the alpine plants at Brintnell Lake.

The plants of wide range on the mountains of Alaska, Yukon, British Columbia, and Alberta may well have had access to the large refuge of the Yukon Plateau and to possible refugia in the northern Rocky Mountains and eastern foothills, as well as to those of Beringia. The smallest ranges are those of the Alaskan species which were probably limited to Beringian refugia.

Nearly all of the forest plants at Brintnell Lake are derived from wide-ranging species in boreal America. I have already noted that only ten of the western plants represented are typically forest types. The Brintnell Lake forest flora is clearly derived from lands to the southeastward and has undoubtedly come up from the Liard valley. That of the central Mackenzie region, in turn, as I have suggested in an earlier paper, has probably developed from the amalgamation of populations that persisted through Late Wisconsin time in the East and in the valleys and foothills of the Rocky Mountains. All of these species could have maintained fairly large ranges during that time, and have no doubt increased their spreading capacity by subsequent fusion of populations.

## ORIGINS OF THE BRINTNELL LAKE FLORA

By way of summary of the foregoing we may picture the Mackenzie Mountains as having been one of the latest montane areas to lose its glaciers (remnants of them still exist). While the glaciers were retreating there was a period of time during which the lower slopes were tundra-covered, with the tundra more or less continuous across the neighboring valleys and to neighboring mountain ranges. The length of the period is problematical. There is some evidence, however, that forests did not come into the lower valleys until about 7,000 years ago, and that they did not cover the divides until somewhat later. In any case the tundra period must have been one in which arctic and alpine plants of all the northwestern refugia had open routes of migration to the Mackenzie Mountains. There is evidence that they availed themselves of these routes in differing proportions, depending first upon their broad habitat preferences, and second upon their inherent abilities to migrate. Their success at colonizing the mountains was conditioned also by the remoteness of the various refugia. Plants of continental habitat preferences were of course most successful; and of these the wide-ranging Arctic-Montane group were outstanding because of both accessibility and lack of biotype depauperation. Survivors in the Yukon valley and the northern Rockies were second in numbers, for they were only partially depauperated and were near at hand. Northern Beringian and Coastal radiants were next in importance, probably held in check by distance and lack of plasticity.

The process of alpine colonization appears to have been checked, at least for the Brintnell Lake region, before it had reached anything like completion. Evidence for this is to be found in the general paucity of species in the alpine plant cover. The "partial" nature of the flora is to be seen in all the common arctic families and genera. Such groups as *Potentilla*, *Senecio*, *Arnica*, and *Pedicularis*, all represented in surrounding regions by half a dozen or so species, have only 2 to 4 species each in the Brintnell Lake district. The colonization appears to have been stopped by the advance of forests into the surrounding valleys. These forests brought a new element to the mountain flora, derived from refugia south of the ice or on the slopes of the more southern mountains. Whether any of it came from the Yukon valley is uncertain. It was derived from Hultén's Boreal Circumpolar, Continental western American and possibly in part from his western coastal groups. In terms of range patterns outlined in this paper it was drawn chiefly from wide-ranging forest species and in part from the "timber-line" group. By nature it is aggressive, but probably shows so small a portion of the total Brintnell Lake flora as it does only because of the short time available for its invasion, and because of the subarctic situation of the Mackenzie Mountains.

## GENERAL CONSIDERATIONS

I would be bold indeed if I were to attempt a detailed correlation of these geobotanical events with those in other boreal and temperate parts of North America. It is impossible, however, to resist the temptation to do a little speculating.

As I have said previously, there is good evidence that there were no forests in most of Alberta, northern Saskatchewan or Mackenzie until the last of the great post-Glacial lakes of the central Mackenzie basin were drained. Using Antevs' chronology, this did not occur until approximately the advent of the post-Glacial optimum, or toward the close of his "younger Late Glacial" period. Similar evidence indicates that there were no forests in the Saskatchewan River basin until Glacial Lake Agassiz had reached nearly the modern level of Lake Winnipeg. The latter event may have occurred somewhat earlier than the drainage of the last Mackenzie basin lakes, but Antevs places it also in the "younger Late Glacial." He suggests that the period of Lake Agassiz may have been 10,000 to 15,000 years in length, and that it corresponded to the period of ice recession from northern New England north to beyond Lake Timiskaming.

If these chronologies are reasonable then it seems necessary to recognize a wide gap in the continuity of the northern coniferous forest, beginning with the advance of the Mankato or Wisconsin<sub>3</sub> ice, and lasting at least until 7,000 or 9,000 years ago. The wide ranges of the forest species described in this paper must have been achieved since that time. In Mac-

kenzie and Yukon we probably are seeing the last stages of this achievement, with the amalgamation of eastern and western relic elements, and the advance of newly aggregated forests into the mountain valleys and adjacent plateaus. When prairies were developing in Ohio, therefore, and when there was, we suppose, a warmer climate in southern New England, forests were just beginning to cover the upper Saskatchewan and southern Mackenzie watersheds, and the alpine areas of the Mackenzie Mountains still had floristic access to the Rockies, Coast Ranges, and the Arctic.

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